Fish assemblages in European lakes - Comparison of sampling methods and analysis of size structure

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This thesis is based on five papers, which are referred to in the text by their Roman numerals (**I**-**V**).

Paper I Heermann, L., **Emmrich, M.**, Heynen, M., Dorow, M., König, U., Borcherding, J., and Arlinghaus, R. (2013): Explaining recreational angling catch rates of Eurasian perch, *Perca fluviatilis*: the role of natural and fishing-related environmental factors. *Fisheries Management and Ecology*, in press.

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Paper II **Emmrich, M.**, Winfield, I.J., Guillard, J., Rustadbakken, A., Vergès, C., Volta, P., Jeppesen, E., Lauridsen, T.L., Brucet, S., Holmgren, K., Argillier C., and Mehner, T. (2012): Strong correspondence between gillnet catch per unit effort and hydroacoustically derived fish biomass in stratified lakes. *Freshwater Biology*, 2436-2448.

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Paper III **Emmrich, M.**, Helland, I.P., Busch, S., Schiller, S., and Mehner, T. (2010): Hydroacoustic estimates of fish densities in comparison with stratified pelagic trawl sampling in two deep, coregonid-dominated lakes. *Fisheries Research* 105: 178-186.

doi: 10.1016/j.fishres.2010.05.001

Paper IV **Emmrich, M.**, Brucet, S., Ritterbusch, D., and Mehner, T. (2011): Size spectra of lake fish assemblages: responses along gradients of general environmental factors and intensity of lake-use. *Freshwater Biology* 56: 2316-2333.

doi: 10.1111/j.1365-2427.2011.02658.x

Paper V **Emmrich, M.**, Pédron, S., Brucet, S., Winfield, I.J., Jeppesen, E., Volta, P., Argillier, C., Lauridsen, T.L., Holmgren, K., Hesthagen, T., and Mehner, T.: Differential pattern of size structure in European lake fish assemblages depending on elevation, latitude and species composition.

Manuscript

Maps were made with Natural Earth: Free vector and raster map data @ naturalearthdata.com

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Paper I This study consists of two parts: a single-lake study and a multi-lake study with different author contributions.

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Paper II All authors contributed with data, **ME** & TM designed the study, **ME** analysed the data and wrote the paper. All co-authors revised the paper.

Paper III All authors contributed with data, **ME** & TM designed the study, **ME** analysed the data and wrote the paper. All co-authors revised the paper.

Paper IV DR created the database, **ME** contributed with data, **ME** & TM designed the study, **ME** & SBr analysed the data, **ME** wrote the paper. All co-authors revised the paper.

Paper V All authors contributed with data, SP created the database, **ME** & TM designed the study, **ME** analysed the data and wrote the paper. All co-authors revised the paper.

Abstract (English)

Lake fish assemblages are increasingly exposed to environmental change in their habitats. The investigation of abiotic and biotic factors and their effects on the size structure of lake fish is essential for predicting the response of fish assemblages to environmental change. However, sampling of lake fish is challenging because sampling gears are selective. The quality and correspondence of fish catches from angling, gillnetting, trawling and hydroacoustics were analysed. Non-standardised catch data from recreational angling were of limited quality for a comparison of fish stocks. Vertical hydroacoustics is an efficient method to quantify fish biomass in stratified lakes. Sampling effort of multi-mesh gillnets can be reduced when fish abundance estimates are derived from contemporarily operating hydroacoustics. Trawling is useful to sample pelagic fish assemblages in deep lakes.

The size structures of fish assemblages differed on a small and a large geographical scale along gradients of abiotic and biotic lake descriptors and differences in fish assemblage composition. At a small geographical scale assemblages in deep and less nutrient-rich lakes with high predator abundances were characterised by a higher proportion of large fish. Shallow nutrient-rich lakes with few predators were characterised by more medium-sized fish. At a large geographical scale thermal optima of fish generated two types of assemblages with different size structures. A high proportion of large salmonids was observed in coldwater lakes at high elevation sites in northern and southern Europe. Lowland lakes with cool- and warmwater fish were dominated by small-sized individuals. The results suggest that lowland lake fish assemblages are relatively robust against environmental change. Coldwater fish assemblages instead may suffer dramatic consequences from global warming as expected species shifts are likely to be accompanied by shifts in the size structure towards smaller individuals.

Key words: lake fish, hydroacoustics, gillnet, trawl net, recreational angling, body size, size structure

Abstract (German)

Fischgemeinschaften in Seen sind zunehmenden Umweltveränderungen unterworfen. Die Analyse des Einflusses abiotischer und biotischer Faktoren auf die Größenstruktur von Fischgemeinschaften ist entscheidend, um die Entwicklung von Seeökosystemen im Zuge von Umweltveränderungen vorhersagen zu können. Es ist jedoch schwierig Fische in Seen zu beproben, da Fanggeräte selektiv sind. Die Qualität und Vergleichbarkeit von Fischfängen durch Angler, Kiemennetze, Schleppnetze und Hydroakustik wurden untersucht. Anglerfänge eignen sich begrenzt für vergleichende Fischbestandsuntersuchungen. Vertikale Hydroakustik eignet sich für die Fischbiomasse-quantifizierung in geschichteten Seen. Der Beprobungsaufwand von Kiemennetzen kann reduziert werden, wenn zeitnah hydroakustische Untersuchungen statt finden. Schleppnetze eignen sich für die Beprobung von pelagischen Fischen in tiefen Seen.

Die Größenstruktur von Fischgemeinschaften unterschied sich auf regionaler und überregionaler Ebene entlang abiotischer und biotischer Gradienten. Die regionale Studie zeigte, dass tiefe nährstoffarme Seen mit hohen Raubfischabundanzen durch mehr große Fische gekennzeichnet waren. Nährstoffreiche Flachseen mit wenigen Raubfischen zeigten höhere Anteile von mittleren Fischgrößen. Im überregionalen Vergleich führten Temperaturpräferenzen der Fischarten zu zwei Fischgemeinschaften, die sich in ihrer Größenzusammensetzung unterschieden. Ein hoher Anteil großer Salmoniden war typisch für hochgelegene Kaltwasserseen im Norden und Süden Europas. Flachlandseen mit Kühl- und Warmwasserfischen zeichneten sich durch eine Dominanz von kleinen Fischen aus. Das lässt vermuten, dass Fischgemeinschaften in Flachlandseen relativ robust gegenüber Umweltveränderungen reagieren. Kaltwasserfischgemeinschaften könnten im Zuge der Klimaerwärmung starken Änderungen unterliegen, da eine Veränderung in der Artenzusammen-setzung von einer Verschiebung in der Größenstruktur hin zu mehr kleinen Fischen begleitet sein wird.

Schlagwörter: Fisch, See, Hydroakustik, Kiemennetz, Schleppnetz, Freizeitangelei, Körpergröße, Größenstruktur

1 Introduction

The following thesis can be divided into two halves referring to different approaches. The first half consists of a methodological and technical approach in analysing the quality and correspondence of fish catches obtained by different types of sampling gear (**papers I**, **II** & **III**; Figure 1a). The second half is primarily related to basic ecological questions, and underlying abiotic and biotic factors and their effects on the size structure of fish assemblages in European lakes were analysed (**papers IV** & **V**; Figure 1b). Both approaches are closely linked, as the conclusions on size structure patterns in lake fish assemblages are derived with the catch data from types from sampling gear presented in the first approach (Figure 1).

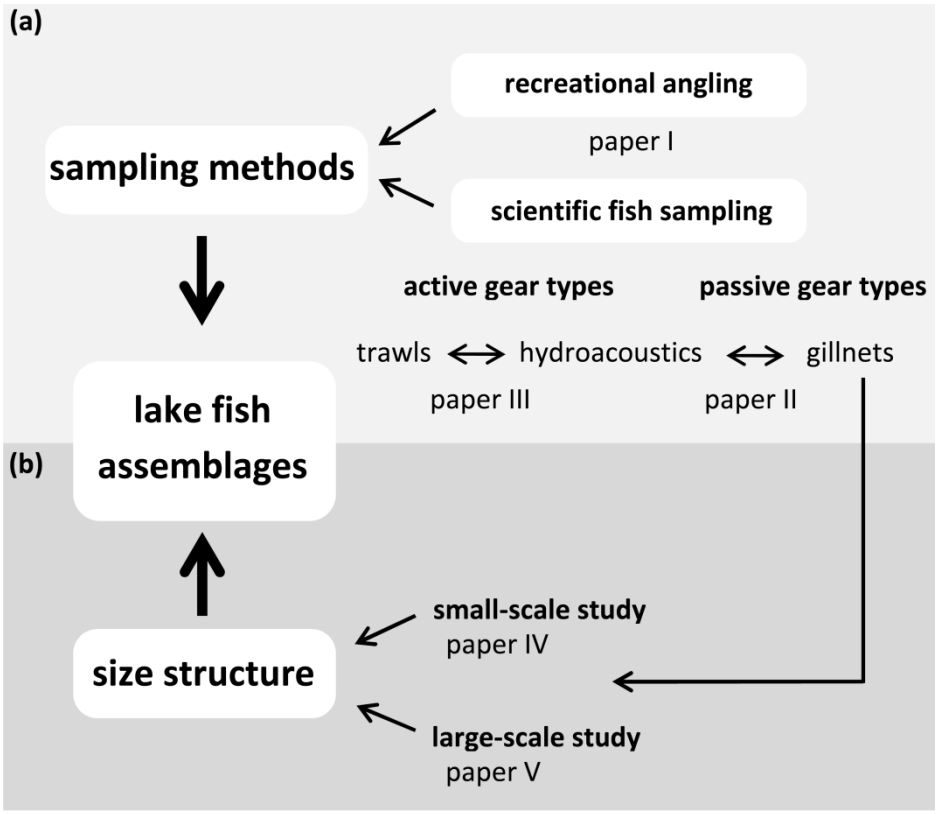

Figure 1: Schematic view of the structure of this thesis which is based on five papers referring to a methodological approach (a) and a size-related approach (b).

Representative sampling of lake fish assemblages is challenging particularly in large lakes (Kubečka et al. 2009). Fish sampling may be efficient in small water bodies such as wadeable streams and shallow ponds (*e.g*. Rosenberger & Dunham 2005), but samplings become more difficult with increasing size and depth of the water body. However, environmental directives such as the Habitat Directive (European Communities 1992) and the Water Framework Directive (European Union 2000) require

an assessment and the monitoring of fish assemblages in large European lakes. An important prerequisite for comparable large-scale fish samplings is the application of standardised sampling methods with comparable post processing and analyses of samples (Bonar & Hubert 2002). Substantial research has been gone into developing, improving and harmonising the standardised scientific types of fishing gear used to sample lake fish (Bonar et al. 2009; Kubečka et al. 2009; 2012). Nevertheless, there remains a strong research demand for studies comparing lake fish catches from different types of sampling gear (Kubečka et al. 2009; 2012). Fish data from standardised samplings are meanwhile available from several hundred lakes located in countries throughout Europe. Merging of these local datasets would provide an excellent premise for comparable and representative studies which may answer current questions in basic and applied research. The availability of such large datasets built the impetus for this thesis.

It is hypothesised that analyses of fish catch data obtained from many lakes using the same types of sampling gear and comparable sampling designs, provide new insights if and how fish catch data from different types of sampling gear correspond to each other (methodological approach). Furthermore, it is suggested that high-resolution datasets of European lake fish assemblages which include information on local fish abundance and individual body size, and which were sampled with standardised types of sampling gear provide new insights how the size structure of lake fish assemblages varies across gradients of abiotic and biotic lake characteristics (size-related approach). Studies which analyse the effects of abiotic and biotic factors on the size structure of organism assemblages are essential for identifying and predicting the response of organism assemblages and ecosystems to environmental change (Petchey & Belgrano 2010; Yvon-Durocher et al. 2011; Gardner et al. 2011).

The current state of scientific research of lake fish assemblage sampling methods and analyses of their size structures is reviewed, and existing knowledge gaps and the resulting specific research questions referred to the five papers of this thesis are addressed the following.

1.1 Sampling fish in lakes

Information on fish assemblages can be obtained from many sources (*cf*. Gabriel et al. 2005). Fish data are taken from literature (Gassner et al. 2005; Brämick et al. 2008; Volta et al. 2011), from obligatory and voluntary catch statistics of commercial and recreational fisheries (Eckmann et al. 2006; Brämick et al. 2008; Gerdeaux & Janjua 2009), and from samplings using scientific types of sampling gear (Peltonen et al. 1999; Jeppesen et al. 2006; Deceliere-Vergès & Guillard 2008). Several

sampling techniques and types of sampling gear have been developed to sample fish in lakes and reservoirs (for reviews see Portt et al. 2006; Bonar et al. 2009) but virtually all types of sampling gear are species- and size-selective (Gulland 1980). The use and comparison of different sampling techniques may help to understand and balance this gear-specific catch selectivity (Dahm et al. 1992; Kubečka et al. 2009).

Fish samplings should ideally be as comprehensive as possible to reflect a 'true picture' of the fish stock (Kubečka et al. 2009) even though depending on the specific research question. Quantitative data are important in fisheries management for instance to regulate planktivorous fish stocks in order to improve water quality in lakes and reservoirs (Jurvelius & Sammalkorpi 1995; Schmidt et al. 2005). Simple presence-absence information may be instead sufficient to describe differences in lake fish assemblage composition across large spatial scales (Heino et al. 2010). Nevertheless, an overall 'true picture' should include information on fish quantity, species composition, size structure, spatial and temporal distribution patterns of the fish and an assessment of data accuracy and data precision (Kubečka et al. 2009). Such a comprehensive description of fish stocks, including a critical data evaluation, is not always possible. Local regulations or limited resources often set strict limits to the choice of types of sampling gear as well as the intensity of sampling and data post processing. Therefore, knowledge about the quality of fish catches from different types of sampling gear, and whether catches from different types of sampling gear are comparable, is crucial in fish science and lake ecosystem management.

1.1.1 Recreational angling

Angling catch records are frequently used to infer insights about fish population structure in lakes (Elliott & Fletcher 2001; Kuparinen et al. 2010; Vainikka et al. 2012), particularly when local restrictions prevent or limit the use of scientific sampling gears such as gillnets (Mosindy & Duffy 2007; Winfield et al. 2009). Anglers' catches are typically expressed as relative catch-per-unit-effort (CPUE) data (*i.e*. number or biomass of fish caught per hour of fishing). However, it remains unknown whether anglers' CPUE data are a reliable measure of fish abundance and population size structure, as anglers' catches are strongly species- and size-selective (Bray & Schramm 2001; Smith 2002; Alós et al. 2009). Fishing skills and fishing experience of individual anglers, as well as the choice of bait type and lure size can influence catch composition, catch rates and size of fish caught (McConnell et al. 1995; Arlinghaus & Mehner 2003; Wilde et al. 2003; Arlinghaus et al. 2008). Furthermore, most angling catch data lack a standardisation (*e.g*. the use of gear and bait type, lure size) comparable to those established for scientific fish sampling methods (*cf.* Appelberg et al. 1995; Bonar et al. 2009; Parker-Stetter et al. 2009). However, standardisation of fish samplings is fundamental to facilitate

the comparison of fish stocks among water bodies (Bonar & Hubert 2002). Many studies which have analysed anglers' catches to assess the status and trend of fish stocks are limited to single water bodies (*e.g*. Lux & Smith 1960; Cooper & Wheatley 1981; VanDeValk et al. 2005). Some research has adopted comparable approaches for analysing catch data from a series of lakes and relating variability in fish catches to differences in abiotic lake characteristics related to lake morphometry, trophic status and productivity (Ryder 1965; Hanson & Leggett 1982; Wilde & Pope 2004a). The understanding whether angling catches can reflect general limnological and morphometric lake characteristics, and how catch data are influenced by individual angler attributes, is important to evaluate the quality of fish catch data from anglers to characterise and to compare fish stocks from a series of water bodies.

Eurasian perch (*Perca fluviatilis* L., hereafter perch) is widespread across Europe (Kottelat & Freyhof 2007) and perch is a highly valuable and strongly targeted angling species in many European countries such as Germany (Arlinghaus & Mehner 2004) and Finland (Vainikka et al. 2012). This makes perch a distinguished model species to test whether angler catches reflect differences in abiotic lake characteristics, and how angler catches are influenced by an individual angler attributes. Perch continuously occurs in shallow and deep lakes along the full trophic gradient from ultra-oligotrophic to hypertrophic lakes (Jeppesen et al. 2000; Beier 2001; Olin et al. 2002). Between-lake population size of perch can differ substantially among lake types reflecting the prevailing abiotic and biotic conditions. High perch abundances are typically observed in relatively deep vegetation-rich lakes characterised by high water transparencies and low to moderate nutrient concentrations. By contrast, low perch abundances are characteristic for eutrophic, less structured and turbid lakes (Persson et al. 1991; Olin et al. 2002; Mehner et al. 2005). It is therefore likely that anglers' catch rates of perch vary among lakes which differ in morphometry and trophic status.

1.1.2. Scientific fish sampling

Fishing gear types are usually classified as either active or passive. Passive types of fishing gear such as gillnets, traps and fyke nets are stationary, and the catching success of the gear depends largely upon the activity and behaviour of the fish encountering the gear, and the probability of being retained in the gear (Hamley 1975; He & Pol 2010). Passive types of fishing gear are most efficient during periods of high fish activity, such as twilight (Vašek et al. 2009; Prchalová et al. 2010). Contrary to this, active types of fishing gear such as trawling, seining and hydroacoustics are moved either by machines or with human power to capture or detect fish. Active types of fishing gear are more efficient at catching slow-swimming and resting fish which are ideally exposed in less structured habitats, for instance fish which migrate into the pelagic lake habitat during darkness (Appenzeller &

Leggett 1992; Lewin et al. 2004; Schmidt et al. 2005). Concerning active types of fishing gear, fish movement is primarily important with respect to fish avoidance reactions from fishing vessels and fishing gears (Draštík & Kubečka 2005; Guillard et al. 2010; Rakowitz et al. 2012). Passive types of fishing gear typically catch fish at a specific location over a prolonged time period, while active types of fishing gear typically catch fish over a larger area during a shorter time period (Portt et al. 2006). Active and passive types of fishing gear are often used simultaneously to obtain a more comprehensive understanding of fish stocks, and to compare gear performances (Olin & Malinen 2003; Olin et al. 2009; Jurvelius et al. 2011).

Data from scientific fish samplings are meanwhile available from several hundred European lakes, mainly based on catches in multi-mesh gillnets (*e.g*. Tammi et al. 2003; Jeppesen et al. 2003; Mehner et al. 2007). Originally developed in the Nordic countries of Norway, Sweden and Finland (Appelberg et al. 1995) NORDIC multi-mesh gillnets have become the official standard for freshwater fish monitoring in European lakes (CEN 2005) (*cf*. *3.1.2.1* for net and sampling details). However, the intensive use of gillnets for sampling lake fish assemblages remains controversial among fish scientists and fisheries managers, as exemplified below.

Similarly to anglers' catches, catches from passive gillnets can only provide relative estimates of fish abundance usually expressed as CPUE data (*i.e*. fish caught per net per night). Relative fish abundance estimates may not entirely correspond with absolute quantitative fish densities (Linløkken & Haugen 2006; Prchalová et al. 2011) because of the species- and size-selectivity as well as the saturation effect of the gillnets, which varies depending on the number of fish entangled in the meshes (Olin et al. 2004; Prchalová et al. 2011). Representative gillnet sampling particularly in large, deep lakes requires considerable effort and subsequent catch processing time, and is therefore costly (Dahm et al. 1992; Van Den Avyle et al. 1995). Some European countries (United Kingdom, Ireland, Netherlands, Belgium) limit or prevent the intensive use of gillnet sampling (Winfield et al. 2009; Harrison et al. 2010) due to a low acceptance by the public and the recreational fisheries community (Winfield et al. 2009). In most situations, gillnets are considered to be destructive, because they kill most fish entangled in the meshes if the nets are left for several hours in water at higher temperatures or rapidly lifted from deep zones to the surface (*cf*. Buchanan et al. 2002). The application of alternative fish sampling techniques using less invasive types of fishing gear is necessary to reduce fish mortality in the course of scientific samplings.

Active types of fishing gear such as trawls and mobile hydroacoustics can provide alternatives to the destructive gillnet sampling. Trawling can reduce fish mortality (Jurvelius et al. 2000; Macbeth et al. 2006) and the application of hydroacoustics even prevents any harm to fish (Simmonds &

MacLennan 2005). Scientific lake fish sampling using trawls is far less frequently applied in Europe, probably because trawls are more difficult to operate compared to other gear such as gillnets (Kubečka et al. 2012). Trawling in often restricted to large, deep lakes, and trawls can best operate in less structured habitats such as pelagic areas to prevent damage to the gear (Peltonen & Horppila 1992). No international standard protocol has yet been developed to guide the scientific sampling of freshwater fish with trawls. However, there is a general consensus towards the importance of such a standard for the future (as illustrated by international researchers who attended the workshop: 'Assigning ground truth to hydroacoustic density estimates - Improving accuracy and precision in fish community assessments', in Stockholm, Sweden, 2011). Fish catches from trawls can be reported in absolute quantitative units (*e.g*. kg ha^{-1}), because the catches can be related to the volume and area sampled by the trawl (Kubečka et al. 2012). Absolute fish density estimates can be superior in situations where a reliable estimate of total fish biomass, fish production, fish yield and an assessment of the ecological integrity of lakes is required (Hanson & Leggett 1982; Jurvelius & Sammalkorpi 1995; Gassner et al. 2003). Trawling can be very efficient in sampling large, deep lakes populated by large stocks of pelagic fish (Haakana & Huuskonen 2008), and trawling may provide a more representative picture of pelagic fish stocks (Olin et al. 2009; Jurvelius et al. 2011) which are poorly sampled by passive types of sampling gear such as gillnets (Deceliere-Vergès & Guillard 2008; Lauridsen et al. 2008; Achleitner et al. 2012).

In contrast to capture-based fishing techniques, data acquisition by remote-sensing techniques such as hydroacoustics is completely non-invasive as it involves no physical contact with the fish. The use of transmitted underwater sound to investigate fish stocks is a rapidly developing field in fish science and fisheries management, and represents an increasingly favoured option to investigate lake fish assemblages (Simmonds & MacLennan 2005; Kubečka et al. 2009). Compared to gillnetting and trawling, hydroacoustic techniques provide a very powerful tool to investigate a substantial volume of water within relatively short time periods (Godlewska et al. 2004). Digital data obtained from modern split-beam echosounders are unprecedented, and allow a detailed analysis of fish abundance, fish biomass, and an analysis of the size structure, the spatio-temporal distribution and behaviour of fish *in situ* (*e.g*. Imbrock et al. 1996; Torgersen & Kaartvedt 2001; Godlewska et al. 2004). However, even state-of-the-art split-beam echosounders cannot distinguish between fish species and vertical downward-looking hydroacoustics have difficulties in detecting fish near the lake surface and bottom boundaries (Simmonds & MacLennan 2005). For these reasons, ground-truth data, *i.e*. biological information derived from capture-based sampling techniques are essential to aid a meaningful interpretation of hydroacoustic data. Fish catch data from both active and passive types of sampling gear are used to analyse the species composition, size and age structure and condition

(fertility, growth rates, etc.) of fish stocks investigated by hydroacoustics (McClatchie et al. 2000). An official standard protocol guiding the application of hydroacoustics to sample fish in European freshwaters (prEN 15910, CEN 2009) has not yet been finished (see Parker-Stetter et al. (2009) for a United States standard). However, guidelines for the standardisation of hydroacoustic methods are already available (Winfield et al. 2011).

Highlighting the continuous improvement of types of scientific sampling gear, sampling methods and survey designs to sample lake fish, there remains a strong research demand for studies comparing relative fish catches obtained from passive types of sampling gear (CPUE data) to absolute fish abundance estimates obtained from active types of sampling gear (Kubečka et al. 2009; 2012).

1.2 Size structure of lake fish assemblages

Variation in body size has long been recognised as one of the most fundamental issues in ecological research (Elton 1927; Brown et al. 2004). Body size plays an important role for most life history attributes of organisms including respiration, growth, maturation and reproduction (Blueweiss et al. 1978; Peters 1983; Calder 1984). Differences in body size influence predation rates and competition between individuals (Brooks & Dodson 1965; Kerr & Dickie 2001). In particular, organism assemblages of aquatic ecosystems are strongly size-structured with substantial size differences between species (interspecific variation) and between the ontogenetic stages of species (intraspecific variation) (Werner & Gilliam 1984; Jennings et al. 2001). This variation in body size leads to complex interactions across multiple levels of ecosystem organisation (Persson et al. 1996) determining predator-prey interactions, body size abundance relationships and energy fluxes in food webs (Emmerson & Raffaelli 2004; Reuman & Cohen 2005; White et al. 2007). Fish play a key role in lakes, with pronounced effects on ecosystem organisation and functioning (Northcote 1988; Carpenter & Kitchell 1996; Jeppesen et al. 1997) mediated through species- and size-selective predation on zooplankton (Brooks & Dodson 1965; Greene 1983), macroinvertebrates (Gilinsky 1984; Blumenshine et al. 2000) and other fish (Sogard 1997; Dörner et al. 1999). Fish predation can promote trophic cascading effects in lakes affecting lower trophic levels such as zooplankton and phytoplankton (Carpenter & Kitchell 1996).

Competition and predation are among the most important biotic interactions influencing the size structure of fish assemblages (Persson 1983; Kerr & Dickie 2001). Strong competition, particularly among juvenile fish, can substantially diminish growth relative to the potential of the species. This is referred to as a trophic bottleneck (Heath & Roff 1996). Food limitation can generate fish

populations that are dominated by dwarf-sized individuals (Ylikarjula et al. 1999). Such stunted populations are frequently observed among many common fish species which populate European lakes, including roach (*Rutilus rutilus* (L.), Burrough & Kennedy 1979; Linfield 1980), bream (*Abramis brama* (L.), Cazemier 1982), perch (Deelder 1951; Linløkken et al. 1996), Arctic charr (*Salvelinus alpinus* L., Janhunen et al. 2010) and whitefish (*Coregonus* lavaretus (L.), Amundsen 1988). Even populations of lake top predators such as pikeperch (*Sander lucioperca* (L.)) may be dominated by dwarf individuals if the ontogenetic diet shift from zooplankton to fish failed due to a lack of suitably sized prey fish (Vinni et al. 2009). Within stunted populations of potentially piscivores such as perch and Arctic charr cannibalistic giants can occur (Claessen et al. 2000; Persson et al. 2003; Byström 2006) in situations of high fish densities and strong size disparities within and between cohorts (Smith & Reay 1991). Interspecific predation is also an important mechanism shaping the size structure of multi-species fish assemblages. Several studies have demonstrated a strong positive correlation of predator size and prey size, with larger prey observed in the presence of many larger predators (Persson et al. 1991; Mehner 2010). Fish are gape-size limited, and this limitation is a linear function of body size (Nilsson & Brönmark 2000; Dörner & Wagner 2003; Dörner et al. 2007). Ingestion in piscivorous fish is limited by a predation window, which is the specific size range of fish which can be preyed upon (Claessen et al. 2002). The range of the predation window depends on inter- and intraspecific variation in prey morphology, which is again closely related with body size (Nilsson & Brönmark 2000; Kekäläinen et al. 2010). Prey growing outside of this window reach a size refuge where they are largely invulnerable to predation (Olson 1996). The type (*i.e*. species) and size of predators strongly shape the size structure of prey. These size- and species-specific interactions have a major impact on the overall size structure of lake fish populations and multi-species assemblages (Brönmark et al. 1995; Persson et al. 1996). A comprehensive analysis of the effects of biotic factors on the size structure of lake fish must ideally contain information on species abundances, a functional classification of the fish according to their feeding modes (*e.g*. piscivorous, non-piscivorous) and information concerning individual body size.

Biotic factors which influence fish assemblage structure interact in complex ways with prevailing abiotic environmental conditions such as the thermal, morphometric and chemical habitat properties (Jackson et al. 2001). The environmental temperature of ectothermic animals has a significant effect on body size, ranging from the individual to the assemblage level (Daufresne et al. 2009), and resulting from physiological constraints at different, species-specific temperature optima (Lindsey 1966; Atkinson & Sibly 1997). The temperature-size rule (Atkinson 1994) describes the phenotypic plastic response of fish body size (and the body size of other ectothermic animals) relative to changes in their environmental temperature. Individuals living in a colder environment grow slowly early in

ontogeny, but mature as larger adults and grow to larger maximum size compared to individuals in a warmer environment (Atkinson 1994). At higher temperatures, early growth is accelerated together with the developmental rate of the individual (Pepin 1991; Johnston & Bennett 1996). This leads to smaller adult body size induced by an early shift of energy allocation from somatic growth towards gonadal development and investment (Blueweiss et al. 1978). The temperature dependence of body size of ectothermic fish is supported by theoretical and empirical evidence from laboratory and field studies (Atkinson 1994; Sibly & Atkinson 1994; Heibo et al. 2005).

The thermal lake regime is determined by the interplay between a lake's geographic location (latitude, longitude, elevation (m a.s.l.)) and morphometry (area, depth) (Edmundson & Mazumder 2002; Williams et al. 2004). Deep lakes and lakes at high latitudes and high elevation are often referred to as cool- and/or coldwater lakes. Lakes which are located at lower elevation sites in central and southern Europe are typically shallower (Nõges 2009), and these lakes can be referred to as warmwater lakes. The lake types can fundamentally differ in fish assemblage composition, controlled by the different temperature optima of coldwater (*e.g*. most salmonids), coolwater (*e.g*. many percids) and warmwater fish (*e.g*. many cyprinids) (Hokanson 1977; Magnuson et al. 1979; Eaton & Scheller 1996). Whether these taxonomic differences in fish assemblage composition cause shifts in the size structure is less understood, particularly across large geographical scales.

Ecosystem size is an important predictor of food-chain length in lakes with more and higher trophic levels in large lakes (Post et al. 2000), and thus larger top predators are typically observed in large lakes. However, mean predator-prey body size ratios are typically smaller in the more stable environment of large ecosystems (Jennings & Warr 2003). Lake depth primarily influences fish assemblage size structure via density-dependent processes. Volumetric fish densities are often lower in deep lakes compared to shallow lakes, leading to on average larger fish in deep lakes (Jeppesen et al. 1997).

A lake's morphometry and thermal regime are furthermore closely linked with lake productivity (Rawson 1952; Brylinsky & Mann 1973). Typically, shallow warmwater lakes have a higher productivity than deep coldwater lakes (Nõges 2009), caused by the rapid recycling of nutrients in the extensive littoral zone (Ryder 1965; Hanson & Leggett 1982). Nutrient-rich warmwater lakes support a higher overall fish biomass and fish density (Hanson & Leggett 1982; Downing et al. 1990; Brämick & Lemcke 2003), and these lakes are often populated by fish assemblages that are dominated by small-sized individuals (Jeppesen et al. 2000; Godlewska & Świerzowski 2003; Teixeira-de Mello et al. 2009). During periods of summer stagnation, fish regularly crowd epilimnetic water layers in shallow and highly productive northern temperate lakes, particularly if environmental

conditions at greater depths are less favourable for the fish (Draštík et al. 2009). This crowding leads to strong biotic interactions in the epilimnion underlying exemplary the close interplay between abiotic and biotic factors in lakes. A comprehensive analysis of the size structure of lake fish assemblages should therefore consider both abiotic and biotic factors.

1.2.1 Anthropogenic influences on the size structure of lake fish assemblages

Today, many lakes are strongly impacted by anthropogenic activities (Mason 2002). Lake fish assemblages are faced with increasing anthropogenically-induced environmental changes in their habitats. An expansion of the socioeconomic value of lake ecosystems has led to the increase pursuit of leisure activities such as boating, bathing, fishing and diving. Lakeshore ecotones in particular are heavily modified by manmade constructions such as beaches, marinas, footbridges, sheet piles and erosion control structures including fascines and rock rip-rap (Strayer & Findlay 2010). Empirical studies have shown that shoreline bank constructions may have a substantial impact on fish assemblage composition, as well as the spatial distribution and growth of fish (Jennings et al. 1999; Schindler et al. 2000; Scheuerell & Schindler 2004). Shoreline bank constructions may furthermore modify entire lake food webs by modifying the quantity and availability of benthic food resources to lake top predators (Doi et al. 2010). Despite this, the possible effects of shoreline degradation and recreational lake-use on the size structure of fish assemblages have yet to be investigated. Fishing can undoubtedly modify the size structure of lake fish assemblages through the species- and size-selective harvesting of primarily larger and predatory fish (Mcdonald & Hershey 1989; Gassner et al. 2003; Lewin et al. 2006). One may therefore anticipate skewed size structures with less large-sized individuals in lake fish assemblages which have been exploited by recreational and/or commercial fisheries.

Anthropogenically-induced eutrophication is still one of the main pressures affecting lake ecosystems (Harper 1992; Mason 2002). Current increases in lake productivity are primarily driven by diffusive nutrient inflows from agriculturally-dominated catchments (Daniel et al. 1998). Eutrophication may downgrade the ecological, economic and recreational value of lakes by reducing biodiversity, altering species composition and decreasing water transparency (Carpenter et al. 1998; Jeppesen et al. 2000; Ansari et al. 2011). Empirical studies have demonstrated shifts in the size structure of lake fish towards a dominance of small-sized cyprinids with increasing eutrophication (Jeppesen et al. 2000). Finally, empirical evidence is accumulating to suggest that global warming, which alters the thermal regime of lakes (*e.g*. Sahoo & Schladow 2008), will play a particularly significant role in modifying species composition, relative species abundances and the size structure of lake fish assemblages

towards an increase and a dominance of warmwater species and small-sized individuals (Lehtonen 1996; Daufresne et al. 2009; Jeppesen et al. 2012).

Analyses of the variations in lake fish assemblage size structure along gradients of lake-use intensity, lake productivity and lake temperature may support predictions of the response of lake fish assemblage structure to future anthropogenic disturbances and environmental changes (*cf*. Petchey & Belgrano 2010).

1.2.2 The role of spatial scale

The spatial scale of a study can determine the relative influence of biotic and abiotic factors on community structure (Declerck et al. 2011). Some factors show large variation at small spatial scales which can generate substantial differences in local communities. Different factors only become important at large spatial scales (Borcard et al. 2004). Small-scale studies, limited in geographical range which are often characterised by relatively stable and comparable environmental conditions among the study sites (*e.g*. climate), indicate a greater importance of biotic interactions such as predation and competition on lake fish assemblage structure (Holmgren & Appelberg 2001; Olin et al. 2010). Large-scale studies which cover broad gradients of abiotic (as well as biotic) factors have instead indicated a stronger influence of abiotic factors (Jackson & Harvey 1989; Jackson et al. 2001) due to an increase in environmental heterogeneity (Zalewski & Naiman 1984).

Local studies which analyse fish assemblage structure in one or several lakes are typically characterised by high-resolution datasets with detailed information on fish abundance, size structure and/or fish habitat use (*e.g*. Lewin et al. 2004). Large-scale studies analysing fish size structure, and involving several hundred lakes are instead typically based on simple presence-absence data and maximum reported fish size, and thus lack detailed information on local fish abundance and individual body size (Knouft 2004; Griffiths 2012). Other studies have focused only on a few selected species, and did not consider entire assemblages (Heibo et al. 2005; Blanck & Lamouroux 2007; Lappalainen et al. 2008). A combination of high-resolution datasets of lake fish assemblages with information on local fish abundance and individual body size (obtained ideally from standardised samplings conducted in several hundred lakes) would therefore provide an excellent premise for investigating the fundamental abiotic and biotic factors which shape the size structure of lake fish assemblages across different spatial scales. Such large datasets from European lakes were not previously available.

Approaches which analyse the effects of biotic and abiotic factors on the size structure of lake fish assemblages at different spatial scales are essential not only for the understanding and identification

of regional and global ecological processes in lakes, but also for identifying and predicting the response of fish assemblages and lake ecosystems to local anthropogenic disturbances and global environmental change (Petchey & Belgrano 2010; Yvon-Durocher et al. 2011; Gardner et al. 2011).

This literature review illustrated current knowledge gaps in research which are related to the sampling of lake fish assemblages and the analysis of their size structure. In summary, studies which analyse the quality of angling catch data collected from European lakes are rare. It is only poorly understood whether non-standardised angling catch data can be used for the characterisation and comparison of fish stocks across a series of lakes. Furthermore, knowledge gaps in scientific fish sampling became evident. Specifically, studies which compare relative fish catch data obtained from passive types of sampling gear (CPUE data) to absolute fish abundance estimates obtained from active types of sampling gear, and which are collected in a standardised manner across a series of lakes are lacking. Sampling fish assemblages using trawls is only infrequently applied in European lakes. Further studies may provide important information about the quality of catch data from trawls and their correspondence to catch data from different types of sampling gear. An increase in knowledge about the efficiency and selectivity of trawl nets may promote the development of an official standard protocol which guide the application of trawls to sample European lake fish assemblages.

Less is known about the biogeographic patterns in the size structure of European lake fish assemblages taking relative fish abundances, differences in species composition, the functional characterisation, individual measures of body size and a range of abiotic descriptors related to the lakes' location, morphometry, productivity and anthropogenic use-intensity into account. Studies which analyse the existing high-resolution datasets on size structure relative to changes in abiotic lake descriptors and differences in fish assemblage composition may lead to an increased understanding which factors influence the structural properties of lake fish assemblages, and how the size structure of lake fish assemblages may respond to future environmental change.

2 Objectives

Regarding to the current knowledge gaps and relating to the two primary objectives of this thesis (*cf*. introduction, Figure 1), the first methodological approach analysed how the quality of anglers' catches reflected abiotic lake characteristics (**paper I**), and tested the correspondence between fish catches obtained from different scientific active and passive sampling methods (multi-mesh gillnetting, trawling and hydroacoustics; **papers II** & **III**, Figure 1a). The second, size-related approach

aimed to investigate differences in the size structure of lake fish assemblages across a small geographical scale (northern Germany, **paper IV**) and across a large geographical scale (eight European countries, **paper V**), both along gradients of biotic and abiotic factors (Figure 1b). Specifically, the five research objectives relating to the five papers of this thesis were:

I) To test whether variations in angling catch data reported in diaries for a series of lakes reflect fundamental lake characteristics related to lake morphometry and trophic status, and to which degree angling catch data were influenced by individual angler attributes.

II) To test the correspondence between relative fish biomass estimates from catches in benthic multi-mesh gillnets and absolute area-related fish biomass estimates derived from vertical downward-looking hydroacoustics (thus comparing passive and active types of sampling gear).

III) To compare absolute abundance estimates of pelagic coregonid-dominated fish stocks derived from vertical downward-looking hydroacoustics and pelagic trawl sampling, taking sampling depth and size of fish caught into account (thus comparing two active types of sampling gear).

IV) To test the applicability of several size metrics derived from benthic and pelagic multi-mesh gillnet catches as a tool to elucidate systematic shifts in lake fish assemblages along environmental (lake morphometry, trophic status, taxonomic and functional fish assemblage composition) and lake-use intensity gradients (a small-scale study).

V) To analyse the biogeographic heterogeneity in the size structure of European lake fish assemblages based on benthic multi-mesh gillnet catches across large ranges of abiotic lake characteristics (geographic location, morphometry, trophic status) and differences in fish assemblage composition (a large-scale study).

3 Methods and datasets

The first study (**paper I**) was based on fish catch data reported from recreational anglers. All other studies analysed fish catch data obtained from scientific samplings using multi-mesh gillnets (**papers II**, **IV** & **V**), vertical hydroacoustics (**papers II** & **III**) and trawls (**paper III**).

3.1 Sampling fish in lakes

3.1.1 Recreational angling

Angling data of perch catches were collected as part of a telephone-diary-mail study aimed to assess the annual fish landings by anglers in northern Germany (Dorow & Arlinghaus 2011). Specifically, randomly recruited anglers fishing regularly in the German state of Mecklenburg Vorpommern were asked to report detailed information from their fishing trips in angling diaries over the course of one year. These diaries included information on the fishing location (water body), targeted species, angling method, bait type, overall and method- and species-specific effort (hours spent fishing), species-specific catch and harvest and the size of the largest fish harvested of a given species. Fishing equipment (*i.e*. the use of rod and reel types and natural vs. artificial bait types) was not standardised and differed among the anglers and water bodies. Angler-specific attributes included fishing skills such as angling experience (in years) and self-rated target species preferences such as predatory or non-predatory fish. **Paper I** incorporates data from lake fishing trips targeting perch for at least some fraction of the fishing trip. Perch catches (CPUE data), as well as the largest size of perch per trip harvested for 143 resident anglers targeting perch in 21 natural lakes in Mecklenburg Vorpommern, were analysed. The CPUE data and size of perch harvested were analysed for environmental lake characteristics (morphometry, trophic status, water transparency), angling skills and angling season.

3.1.2 Scientific fish sampling

3.1.2.1 Multi-mesh gillnets

Most data analysed in this thesis were derived from fish catches in standardised multi-mesh gillnets (**papers II**, **IV** & **V**). The European standard protocol EN 14757 for sampling fish in lakes with NORDIC multi-mesh gillnets (CEN 2005) involves a stratified random sampling design. Lakes are divided into a maximum of eight depth strata (0-2.9 m, 3-5.9 m, 6-11.9 m, 12-19.9 m, 20-34.9 m, 35-49.9 m, 50-74.9 m and depths ≥ 75 m) ideally representing approximately equal volumes of water. Depending on lake area and maximum depth, predetermined numbers of benthic gillnets are set at different depth strata with random positioning and angles of the nets relative to the shoreline. Sampling efforts (*i.e*. the number of nets) ranged typically between eight gillnets per night up to 64 gillnets per night in deep and large lakes with surface areas of approximately 5 000 hectares. In small lakes (< 50 hectares) and in countries with low acceptance of gillnet sampling (*e.g*. U.K.), however, gillnet effort was reduced. To maximise catch efficiency of the nets, sampling should take place between late summer and early autumn before the usual reduction of epilimnion water temperatures to below

15°C (*cf*. Linløkken & Haugen 2006; Dennerline et al. 2012). During late summer and early autumn most European freshwater fish do not spawn or aggregate and young-of-the-year fish are large enough to be caught by the smallest mesh sizes. Gillnets are set overnight for approximately twelve hours to ensure that the activity peaks of many species during dusk and dawn are included (Vašek et al. 2009; Prchalová et al. 2010).

Two types of nets (benthic net and pelagic nets) are used in the standardised fish samplings. Benthic multi-mesh gillnets are made of non-coloured monofilament nylon, are each 30 m long and 1.5 m deep (=45 m^2), and consist of 12 panels of 2.5 m each with mesh sizes ranging from 5 to 55 mm knot to knot (bar mesh size). Thread diameters are 0.10 mm (5-8 mm meshes), 0.12 mm (10 & 12.5 mm meshes), 0.15 mm (15.5 & 19.5 mm meshes), 0.17 mm (24 & 29 mm meshes), 0.20 (35 & 43 mm meshes) and 0.25 mm (55 mm mesh). The order of mesh sizes followed the theory of a geometric series (Regier & Robson 1966) with an almost constant ratio between two adjacent different mesh sizes of approximately 1.25 (Figure 2).

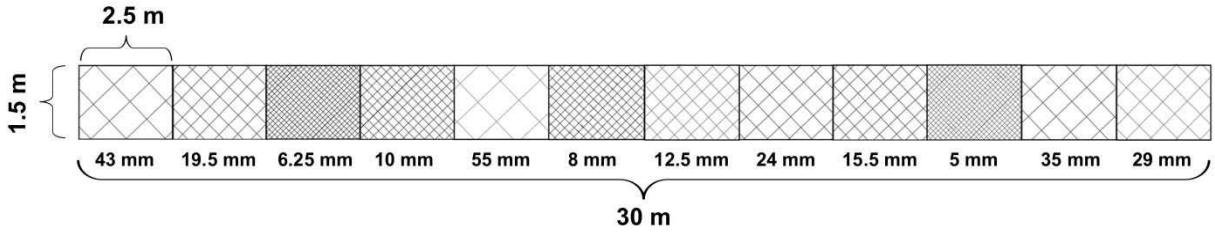

Figure 2: Schematic view of a benthic multi-mesh gillnet

As all fishing gears, also the NORDIC type of multi-mesh gillnets is species- and size-selective (Prchalová et al. 2008; 2009). Specifically, abundances of small fish up to 10 cm long are underestimated (Olin & Malinen 2003; Olin et al. 2009; Prchalová et al. 2009). Small fish generally move less and are consequently less effectively caught by passive stationary gillnets. Furthermore, small fish are less frequently retained by meshes due to their slower swimming speed and the lower flexibility of the smallest meshes, which is caused by the small ratio between thread diameter and mesh size (Hamley 1975). Selectivity curves and correction factors were developed for the NORDIC type of multi-mesh gillnets for a few widespread fish species populating European lakes (Kurkilahti et al. 1998; Finstad et al. 2000; Prchalová et al. 2009). However, existing selectivity curves cannot be extrapolated beyond the length range of the fish for which they were originally fitted (Kurkilahti & Rask 1996). Gillnet catches were thus not corrected for species and size selectivity (**papers II**, **IV** & **V**). In order to reduce the size selectivity for small fish, individuals < 8 cm total length were excluded from the catches (**papers IV** & **V**). This exclusion furthermore minimises potential bias in the size

structure caused by variations in the recruitment success of fish and differences in sampling time and, hence, the length of effective growing season of juvenile fish.

According to the European standard, deep lakes with maximum depths greater than ten meters should additionally be sampled by pelagic multi-mesh gillnets (CEN 2005). Pelagic nets consist of the same material and order of mesh panes as the benthic ones, but lack the 5 mm mesh panel. Pelagic nets are 27.5 m long and 6 m deep (= 165 m^2), and are deployed as a single vertical row from the lake surface to the bottom at the deepest lake part. The sampling effort associated with pelagic nets is fixed, and depends only on the maximum lake depth and not on lake area or volume. Catches from pelagic gillnets were only included in the small-scale study (**paper IV**) because they were not consistently used among the European countries (**papers II** & **V** are based on catches from benthic nets only).

3.1.2.2 Trawling

Pelagic fish samplings using a midwater otter trawl (Figure 3) were performed in two oligo-mesotrophic lakes in northern Germany over a period of four years (**paper III**). The two deep lakes (> 20 m mean depth) are populated with pelagic fish assemblages dominated by coregonids (*Coregonus* ssp.).

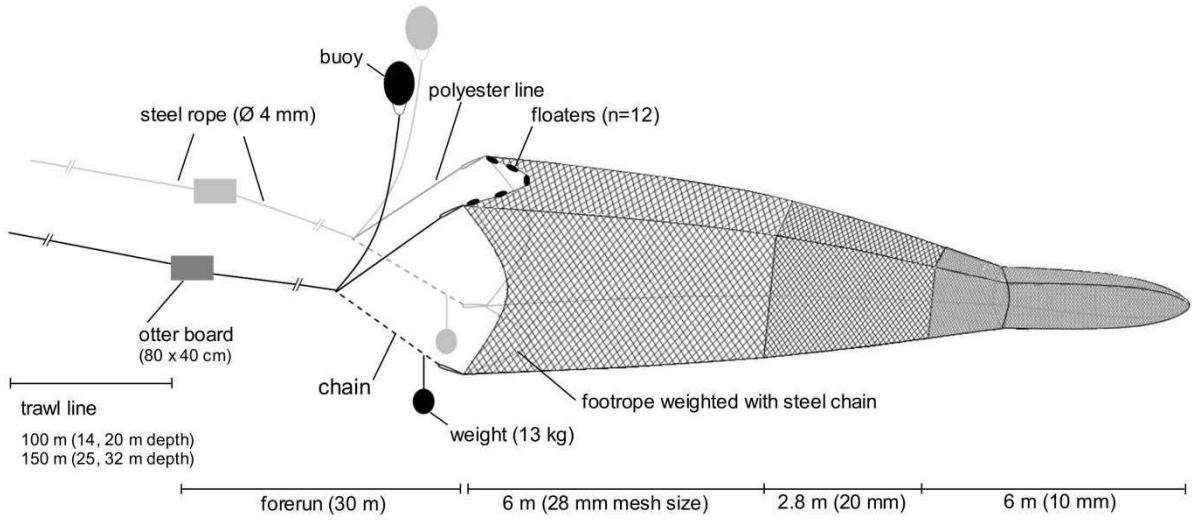

Figure 3: Schematic view of the otter trawl used to sample coregonids

Trawling was conducted in the open water overnight at four different depths between approximately 12 and 32 m. Absolute pelagic fish biomass estimates calculated from the trawl catches were compared with absolute fish biomass estimates and the size distribution of fish sampled by

simultaneously operating hydroacoustics (*cf*. *3.1.2.3*). Furthermore, fish abundances separated into four size classes were compared along the depth gradient between the two types of active sampling gear.

3.1.2.3 Hydroacoustics

Hydroacoustic data were collected by vertical mobile hydroacoustics using downward-looking split-beam echosounders (**papers II** & **III**). Only data from night-time fish samplings were analysed. The survey design was comparable among the 20 lakes (18 lakes **paper II**; 2 lakes **paper III**), and consisted of non-overlapping parallel transects crossing the deeper lake parts. Post processing of the hydroacoustic data was done using the Sonar 5Pro Software, version 5.9.7 (Balk & Lindem 2007, **paper III**) and version 6.01 (Balk & Lindem 2011, **paper II**).

A SIMRAD EY-60 split-beam echo sounder (operating at a frequency of 120 kHz) was used to sample the pelagic coregonid populations of two lakes in northern Germany (**paper III**) (*cf*. *3.1.2.2*). Data from vertical hydroacoustics (and catches from benthic multi-mesh gillnets; *cf*. *3.1.2.1*) were compiled from 18 natural lakes located in seven European countries (**paper II**). All lakes were sampled by hydroacoustics on dates close to the time period of gillnet sampling. Hydroacoustic equipment by different manufacturers (SIMRAD, Simrad Kongsberg Maritime AS, Norway and BIOSONICS, Biosonics Inc., U.S.A.) with slightly different technical settings (sound frequency, pulse duration, sample interval, transmission power) were used. It has been shown that parameters lying within the range of the study (**paper II**) produce unbiased fish biomass estimates (Guillard et al. 2004; Godlewska et al. 2009; 2011). Fish biomass estimates were compared between the active (hydroacoustics) and passive type (gillnets) of sampling gear. Separate analyses were conducted in different depth strata *a priori* defined according to the gillnet standard (CEN 2005) and for several fish-length thresholds to account for the size selectivity of the gillnets (*cf*. *3.1.2.1*).

3.2 Size structure of lake fish assemblages

Several size-based approaches have been developed to analyse the size structure of aquatic organism assemblages (*e.g*. Sheldon et al. 1972; Vidondo et al. 1997; Quintana et al. 2008). A strong research focus has been set on the analysis of zooplankton and phytoplankton size spectra (Sprules & Munawar 1986; Gaedke 1992; De Eyto & Irvine 2007) and studies analysing the consequences of commercial fisheries on the size structure of marine fish stocks (Pope & Knights 1982; Murawski & Idoine 1992; Rochet & Trenkel 2003). The size structure of freshwater fish in lakes has been less intensively studied (but see Holmgren & Appelberg 2000; De Leeuw et al. 2003).

Papers IV & **V** followed a non-taxonomic size approach (*cf*. Damuth 1992), where body size of individual fish was analysed independently of taxonomy. A taxon-free approach is advantageous to large-scale, comparative approaches where structural assemblage properties are analysed and many species are replaced by others along the biogeographic gradients. However, taxonomic (*e.g*. species richness, species composition) and functional (*e.g*. predatory fish, prey fish) fish assemblage characteristics were included as co-variables to test the effects of differences in species composition and predator-prey interactions on size structure. Variations of several size metrics calculated from individual fish lengths and fish weights were related to the variability of abiotic and biotic lake descriptors.

In total, the size structure of fish catches from 707 lakes sampled by standardised multi-mesh gillnets (*cf*. *3.1.2.1*) were analysed (**papers IV** & **V**, Figure 4).

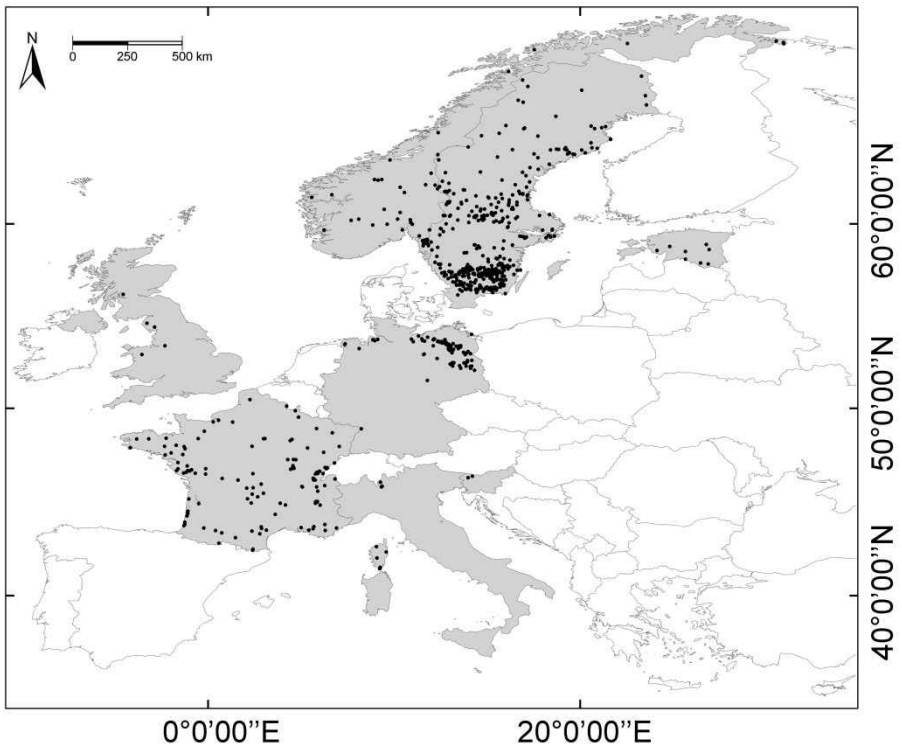

Figure 4: Geographical distribution of the 707 lakes across eight European countries (grey-coloured) whose fish assemblages, sampled with multi-mesh gillnets, were analysed for differences in size structure

These lakes, distributed across eight European countries, covered a latitudinal range of 28° and a longitudinal range of 35°. High-resolution datasets included information on relative abundances of local fish species as well as individual measures of body size, and were available for all lakes. Fish catches were combined with a set of lake descriptors related to lake morphometry, lake use-

intensity, lake productivity, geographic location and differences in taxonomic and functional fish assemblage composition.

In the small-scale study (**paper IV**) fish catches in benthic and pelagic multi-mesh gillnets from 78 lowland lakes in northern Germany were analysed. The lakes are located in the European Central Plains ecoregion (according to Illies' ecoregions classification for rivers and lakes, Illies 1978) which is characterised by moderately continental climatic conditions (Figure 5). The lakes strongly differed in size (area, depth) and trophic status, ranging from oligotrophic to hypertrophic lakes. A total of 17 abiotic and biotic descriptors related to lake morphometry, lake productivity, lake-use intensity and taxonomic and functional fish assemblage composition were available.

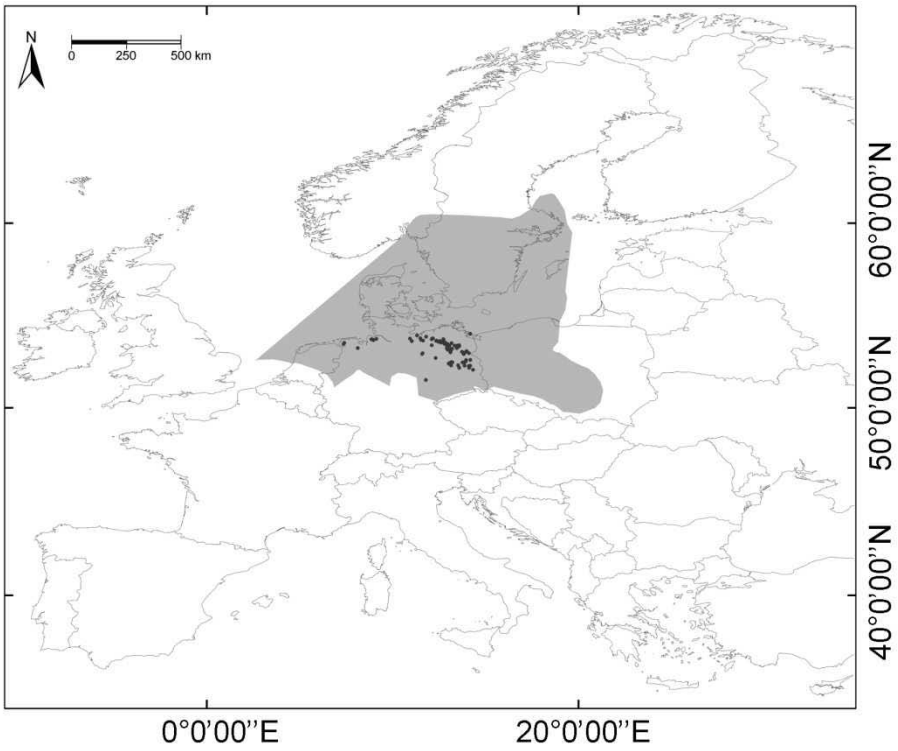

Figure 5: Geographical distribution of the 78 northern German lakes located in the European Central Plains ecoregion (shaded area) whose fish assemblages, sampled with benthic and pelagic multi-mesh gillnets were analysed for differences in size structure (small-scale study). Ecoregion definition following Illies (1978)

The large-scale study (**paper V**) included fish catches of 701 lakes (including 72 lakes from the northern-German dataset) sampled by benthic multi-mesh gillnets. The lakes were selected from a European lake database compiled within the WISER project (Water bodies in Europe - Integrative Systems to Assess Ecological status and Recovery, *cf*. Caussé et al. 2011). For further database

information see Schmidt-Kloiber et al. (2012) and the WISER web page (http://www.wiser.eu /results/metadatabase/). The lakes were located in eight European countries across twelve ecoregions (Illies 1978) with fundamentally different climates representing a gradient from subtropical to subpolar climates (Figure 6). Ranges of morphometric and trophic lake variables were larger than those in the small-scale study (**paper IV**). Variability in the size structure of the 701 lake fish assemblages was analysed along gradients of lake location, lake morphometry, trophic status and differences in fish assemblage composition.

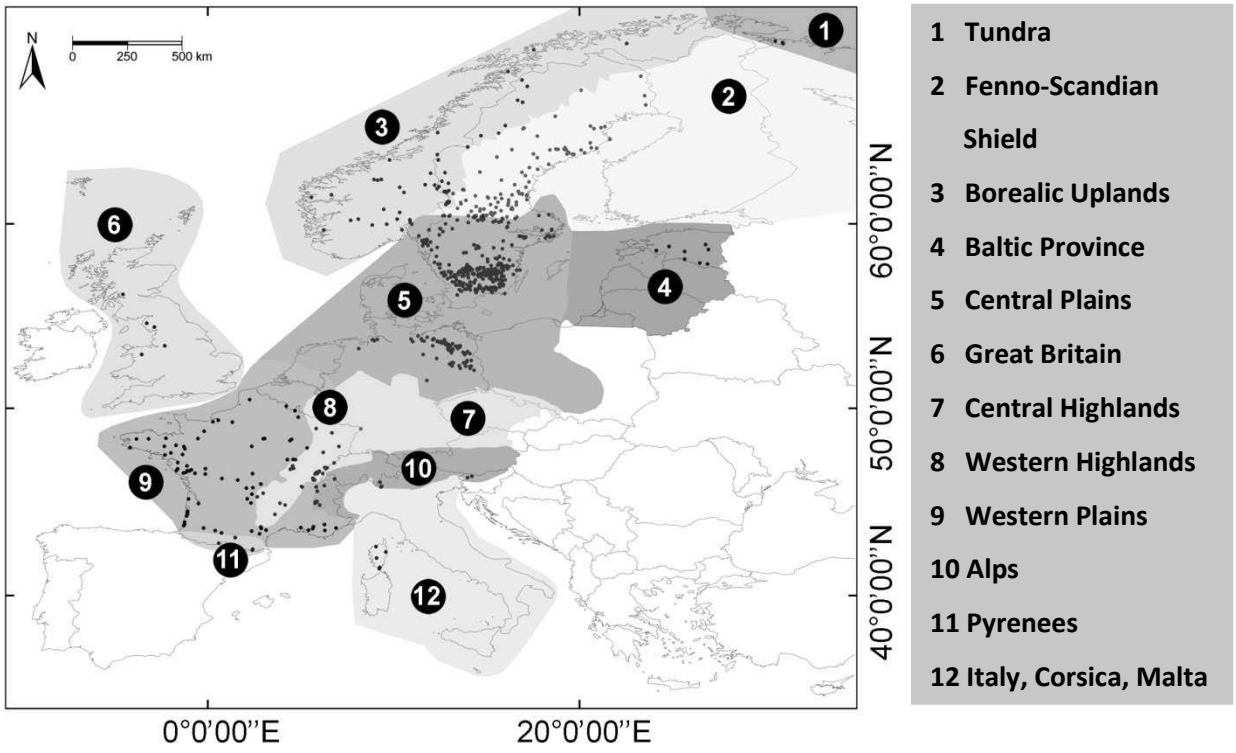

Figure 6: Geographical distribution of the 701 European lakes across twelve ecoregions whose fish assemblages, sampled with benthic multi-mesh gillnets, were analysed for differences in size structure (large-scale study). Ecoregions definitions following Illies (1978)

4 Main results

4.1 Sampling fish in lakes

The studies analysing the quality and correspondence of fish catch data obtained from four types of sampling gear showed very different results. Variations in perch catches by recreational rod-and-reel angling (**paper I**) were strongly affected by individual angler attributes such as fishing skill, fishing experience and bait type. Anglers with a high level of fishing experience, and who specialised in

catching predatory fish such as perch, pike (*Esox lucius* L.) and pikeperch, caught more and larger perch than less experienced anglers, and anglers primarily targeting non-predatory fish such as carp (*Cyprinus carpio* L.), bream and roach. The size of perch harvested was mainly influenced by bait type. Natural baits caught generally larger perch than artificial baits. The variability in anglers' perch catches furthermore weakly reflected abiotic lake characteristics, relating primarily to the trophic status of the lakes. Specifically, higher perch catch rates and larger individuals were observed in oligotrophic lakes and in lakes of intermediate water transparency. Lake morphometry (area, depth) had no significant influence on catch rate and size of perch caught by anglers.

Analyses of fish catch data from scientific samplings (**papers II** & **III**) provided fundamentally new results which are relevant for the selection of types of sampling gear and for the planning of survey designs to sample lake fish. The comparison of relative catches from benthic multi-mesh gillnets and absolute fish biomass estimates from vertical hydroacoustics is among the first studies conducted across a series of lakes that demonstrates a significant relationship between fish catches obtained from passive and active types of sampling gear (**paper II**). Relative fish biomass estimates (CPUE data) calculated from the multi-mesh gillnet catches were significantly log-linear correlated with absolute fish biomass estimates (kg ha^{-1}) obtained from vertical hydroacoustics when very deep lakes (> 30 m mean depth) were excluded. The strength of correlation was independent of the fish length thresholds applied, but varied across different depth strata. The strongest correlation was observed by combining the fish biomass estimates at shallow depth strata. The correspondence between fish biomass estimates from the two types of sampling gear decreased with increasing lake depth. An ordinary least square (OLS) regression to predict absolute lake-wide fish biomass from relative gillnet catches (CPUE data) indicated a reduced reliability at high fish densities. An additional OLS regression line was calculated to predict the absolute fish biomass from gillnet catches at shallow depth strata, and this indicated that lake fish biomass was likely underestimated by vertical downward-looking hydroacoustics.

Fish catches obtained from two types of active fishing gear may produce similar absolute fish abundance estimates (**paper III**). Areal biomass estimates of pelagic coregonid-dominated fish assemblages sampled with trawls and vertical downward-looking hydroacoustics were comparable and did not differ significantly from unity. Depth- and size-specific comparisons revealed significant differences between both gears. Specifically, with increasing fishing depth of the trawl a trend for higher fish abundance estimates was detected by the trawl. Abundances of very small and very large fish were underestimated by the trawl relative to the abundance estimates of these size classes

obtained from hydroacoustics. The trawl used to sample pelagic fish in two deep coregonid-dominated lakes (**paper III**) efficiently caught coregonids with total lengths between 6.5 and 17.5 cm.

4.2 Size structure of lake fish assemblages

The size metrics calculated from fish catches in multi-mesh gillnets characterised specific components of the overall size structure of lake fish assemblages including average size, size diversity, maximum size and the ratio between small and large fish (**papers IV** & **V**). Variability of the size metrics significantly corresponded to variations in abiotic and biotic descriptors of European lakes and their fish assemblages. However, the relative influence of abiotic and biotic factors differed depending on the spatial scale of the study.

Variability in the size structure of lake fish assemblages at a small geographical scale, based on fish samplings of 78 lakes located in northern Germany (**paper IV**) was significantly correlated with differences in lake morphometry (area, depth), trophic status (total phosphorous and chlorophyll *a* concentrations) and functional fish assemblage descriptors (predator abundance, predator-prey length ratio (PPLR)). Fish assemblages in large, deep and less nutrient-rich lakes with high predator abundances and large PPLR were characterised by a higher proportion of large fish and larger maximum-sized fish. In contrast, shallow nutrient-rich lakes with few predators and a low PPLR were characterised by more medium-sized fish. No variable related to the lake-use intensity (fishing pressure, shoreline modification, intensity of recreational activities) significantly corresponded to variations in the size metrics.

Across a large geographical scale, based on fish samplings of 701 European lakes (**paper V**), lake temperature as determined by lake location (*i.e*. elevation, latitude) and lake area were the primary abiotic variables to account for differences in the size structure of fish assemblages. Lake productivity had a very weak influence on variation in the size structure in this large-scale dataset. On average, larger fish were observed at higher-elevation lakes in northern and southern Europe. Large lakes were populated by the largest maximum-sized fish. Species shifts along the elevation gradient and latitudinal gradient generated two types of fish assemblages which fundamentally differed in their size structure. A surprisingly high homogeneity was observed in the size structure of fish assemblages in European lowland lakes dominated by coolwater and warmwater fish such as perch and roach (Figure 7). In these lakes small, juvenile fish were dominant. Significantly higher relative proportions of large fish were observed in lakes whose fish assemblages were dominated by coldwater salmonids. These lakes were mainly located at higher-elevation sites in northern and southern Europe (Figure 7).

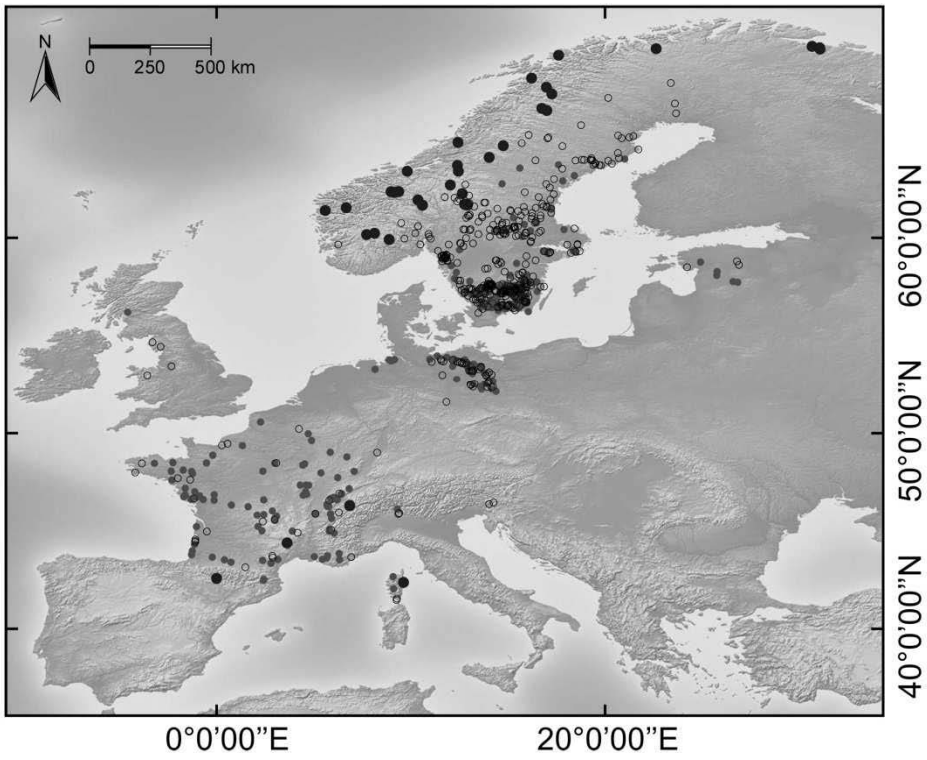

Figure 7: Classification of fish assemblages of the 701 European lakes according to their dominant thermal guild (large filled circles: coldwater fish; small empty circles: coolwater fish; small filled circles: warmwater fish)

5 Discussion

5.1 Sampling fish in lakes

Catches by recreational angling (using perch as a model species) were strongly affected by individual angler attributes. The increase in fishing success (*i.e*. a higher CPUE) with increasing angling experience, outlined in **paper I**, has already been reported elsewhere (McConnell et al. 1995; Arlinghaus & Mehner 2003) and reflects that increasing skill levels are required to catch many and/or certain types of fish (*e.g*. predatory fish, non-predatory fish). Beardmore et al. (2011) demonstrated a similar positive correlation of angling experience and CPUE. Trophy anglers with meanly about 24 years of fishing experience exhibited the highest catch rates and retained, on average, larger fish than other angler groups. The size of perch captured was less controlled by the anglers which was indicated by the poor predictive power of the model on variation in the size of perch harvested by

anglers. Likewise, Wilde & Pope (2004b) reported a very low probability of anglers to catch record-sized fish. Size of perch harvested in the 21 natural lakes located in Mecklenburg Vorpommern, Germany (**paper I**) was primarily influenced by bait type. Natural baits tended to catch larger perch. Large and more experienced perch are thus likely more susceptible to natural baits. It has been demonstrated that repeatedly fishing with artificial baits reduces the catchability of piscivorous fish, whereas catch rates with natural baits do not decrease to lower levels (Beukema 1970; Kuparinen et al. 2010). Avoidance of artificial baits through learning over time especially for visually foraging fishes such as perch (Diehl 1988), may be more pronounced in large individuals. Variation in anglers' catch rates only weakly reflected differences in the lake trophic status and water clarity. In line with expectations and supporting empirical findings on perch population size in lakes, higher perch catch rates were observed in lakes with low nutrient concentrations and high to medium water transparencies. Perch is often the most dominant species in such lakes (Jeppesen et al. 2000; Olin et al. 2002; Radke & Gaupisch 2005). Furthermore, the largest perch were caught in oligotrophic lakes with higher water transparencies. Such nutrient-poor lakes are typically populated by a greater number of large-sized fish (*cf*. **paper IV**).

The strong effect of individual angler attributes related to fishing skills and bait choice on catch rate and size of perch caught by rod-and-reel recreational angling suggests only a limited utility of anglers' catch data to compare fish stocks across a series of lakes. The reliability of such data depends strongly upon which angler type is reporting the data. For single lakes angling catch data may reliably detect changes in structure and size of fish stocks if fishing pressure and angler types reporting the data are comparable between years (Gerdeaux & Janjua 2009). To improve between-lake comparability of angler catch data additional information on lure/bait size, which was not recorded in this study (**paper I**) may improve a quality assessment of angler catch data. Lure size can strongly affect size of fish caught, and small fish are typically less often caught with large lures (Wilde et al. 2003; Arlinghaus et al. 2008). Information of total angling pressure and fishing effort (*e.g*. hours of fishing per hectare per year, *cf*. Mosindy et al. 1987) and knowledge about the angler types who are reporting the data could further aid the interpretation of angling catch data and may improve comparability of such data among several water bodies.

Catch data from scientific samplings can adequately characterise lake fish assemblages and different types of sampling gear can produce comparable estimates of fish abundance. Fish biomass estimates obtained from passive and active types of fishing gear can significantly corresponded to each other (**paper II**), yet a correspondence between relative and absolute fish abundance estimates was generally weak (*e.g*. Peltonen et al. 1999; Prchalová et al. 2012; Dennerline et al. 2012). Olin et al.

(2009) has demonstrated a significant correlation between relative fish abundance estimates derived from gillnets and absolute fish abundance estimates obtained from trawling when small fish were excluded from analyses. Likewise, Mehner & Schulz (2002) reported a significant correlation between fish abundance estimates from gillnets and vertical hydroacoustics when fish from the lower and upper end of the size spectrum were excluded. However, it remains questionable whether results from case studies conducted at single lakes could allow for general conclusions which could be applied to other lakes with different abiotic and biotic conditions.

A weak correspondence of fish abundance estimates between multi-mesh gillnets and vertical hydroacoustics is particularly apparent in deep lakes (Jurvelius et al. 2011), even when fish samplings are conducted across a series of lakes of comparable trophic status (Achleitner et al. 2012). This weak relationship is primarily due to a decreased precision of abundance estimates for pelagic fish from gillnets (*cf*. Deceliere-Vergès et al. 2009; Achleitner et al. 2012). Such fish are, however, reliably detected by vertical downward-looking hydroacoustics. The good correspondence between relative and absolute biomass estimates from gillnet catches and hydroacoustic fish detections, demonstrated in **paper II**, is explained by the size of the underlying dataset, along with fish sampling details and subsequent data analyses (described below).

Firstly, the study represents one of the largest datasets of stratified lakes (n = 18) sampled by multi-mesh gillnets and vertical hydroacoustics ever compiled. The lakes covered large gradients of area, depth, trophic status and fish productivity. Due to the large sample size it was possible to treat entire lakes (rather than several or even single gillnets and hydroacoustic transects within a lake, *cf*. Dennerline et al. 2012) as a single sample unit. By averaging catch data from multiple gillnets and hydroacoustic transects, one improves the comparability of fish samplings between lakes (*cf*. Van Den Avyle et al. 1995). This is due to the substantial reduction in reliance on fish catch data from individual gillnets and hydroacoustic transects, which can be highly variable both horizontally (area) and vertically (depth) (Vondracek & Degan 1995; Vašek et al. 2009; Deceliere-Vergès et al. 2009). Secondly, fish assemblages were sampled by both gear types at dates close to each other. The standing crop and the distribution of fish in lakes can vary in the course of a year (Vijverberg et al. 1990; Winfield et al. 2007; Bobori & Salvarina 2010). Consequently, weaker correspondence in fish catches is observed when samplings are conducted using different gear types at different seasons (*cf*. Achleitner et al. 2012). Thirdly, this study estimated total fish biomass and not numerical fish abundance. Total biomass is a less variable descriptor than numerical abundance, since very small fish (which are abundant but have only small individual masses) and very large fish (which have a high individual mass but are rarer) are both only minor contributors to the overall biomass of lake

fish assemblages. The standing crop of fish stocks is typically primarily composed of intermediate-sized fish (De Leeuw et al. 2003).

These encouraging results from the comparison of an active and a passive type of sampling gear, outlined in **paper II**, support the more frequent application of vertical hydroacoustics to quantify fish biomass in stratified lakes. Gillnetting should be limited to inventory sampling, *i.e*. collecting ground-truth data rather than calculating relative fish abundances (CPUE data), when fish assemblages being sampled by contemporarily operating hydroacoustics. Ground-truth data from a reduced set of gillnets can supplement the hydroacoustic data by providing information on fish assemblage composition, fish condition, size and age structure (McClatchie et al. 2000; Dennerline et al. 2012).

The comparison of catches from benthic multi-mesh gillnets and fish detected by vertical hydroacoustics (**paper II**) supported findings from previous studies which demonstrated that deep lakes with separate pelagic-dwelling salmonids such as coregonids, trouts (*Salmo trutta* ssp.) and charr are not adequately sampled by benthic and pelagic multi-mesh gillnets, independently of whether the European standard EN 14757 (CEN 2005) or a higher sampling effort was applied (Deceliere-Vergès & Guillard 2008; Jurvelius et al. 2011; Achleitner et al. 2012). According to Degermann (1988), 16 pelagic gillnets per depth stratum should result in a comparable degree of accuracy for relative fish abundance estimates as is provided by benthic nets. However, such a high sampling effort is laborious and expensive, and one cannot exclude the possibility of a significant reduction of fish stocks due to the high fish mortality in gillnets (*cf*. 1.1.2). Although a regression line was developed to roughly estimate absolute lake fish biomasses from relative gillnet catches (**paper II**), this regression line cannot be used to predict fish biomass from gillnet catches in very deep lakes, as it was developed with data from moderately deep lakes with no large stocks of pelagic-dwelling fish.

Pelagic fish stocks in deep lakes can be efficiently sampled using trawls (**paper III**). Trawling may provide absolute fish biomass estimates comparable to those obtained by vertical hydroacoustics if the survey design, sampling techniques and data analyses are sufficiently developed (*cf*. Yule et al. 2009). When samplings are simultaneously conducted within the same habitat, the biomass estimates of pelagic fish can be reliably estimated from different types of active sampling gear. A weak correspondence between trawl catches and hydroacoustic fish abundance estimates with substantially lower fish abundances calculated from the trawl catches has been reported elsewhere (Mason et al. 2005; Jurvelius et al. 2005; Stockwell et al. 2007). The equal or even higher fish abundances calculated from trawl catches of pelagic coregonids from two deep lakes (**paper III**) can be explained by technical features of the trawl operation. The otter trawl (Figure 3) was lifted at boat

speeds comparable to the speed of the towing runs of the net. This technique should reduce the chance for fish to escape from the trawl during lifting, as is often observed when a vessel stops (Schmidt 2009). The high net speed during lifting, however, likely led to additional fish catches by the trawl. This resulted in higher fish biomass estimates, particularly from deep depth layers, compared to hydroacoustically obtained fish abundances for these layers. Furthermore, size-selective constraints of trawls at the lower and upper end of the fish size spectrum are relevant to the analysis of fish size structure and estimates of fish biomass (*cf*. Mason et al. 2005; Říha et al. 2012). Very small and very large fish are not efficiently caught by trawls, because very small fish escape through the meshes (Suuronen et al. 1995; Mous et al. 2002) and very large fish avoid and escape the trawl due to their higher swimming speed (Schmidt 2009; Rakowitz et al. 2012). These size-selective constraints must be taken into account when sampling fish with trawls.

5.2 Size structure of lake fish assemblages

Substantial variation was observed in the size structure of European lake fish assemblages sampled by standardised multi-mesh gillnets. Non-taxonomic size metrics can be used for an identification of systematic variations in the size structure of lake fish assemblages along biotic and abiotic gradients at both small (**paper IV**) and large (**paper V**) geographical scales. However, the relative importance of abiotic lake characteristics and biotic factors is scale-dependent.

Neither at a small scale (**paper IV**) nor at a large scale (Emmrich et al. 2012) significant influence of variables relating to the anthropogenic effects of shoreline modifications, and variables characterising lake-use intensity for recreation was observed. All variables on lake-use intensity and variables related to the impact of manmade structures were categorical in these studies. Categorical data are obviously insensitive to changes in the size structure of lake fish assemblages at least when their effects are tested together with a set of continuous variables in the same analysis (*cf*. Mehner et al. (2005) for a comparable weak effect of categorical lake-use intensity data on lake fish assemblage composition). Alternatively, the degree of anthropogenic disturbances is too weak in the European lakes analysed. Lakeshore ecotones of many north American lakes have experienced a much higher degradation by manmade structures and recreational activities, and strong effects on fish assemblage composition and the spatial distribution and growth of fish have been observed in these systems (Jennings et al. 1999; Schindler et al. 2000; Scheuerell & Schindler 2004).

The small- and the large-scale study both indicated that lake area is an important variable in determining the number of large fish sizes and the maximum fish size in lakes (*cf*. Holmgren &

Appelberg 2000; Wilde & Pope 2004a). Specifically, more large fish and larger maximum-sized fish were observed in large lakes (**papers IV** & **V**). Lake size determines food chain length in lakes (Post et al. 2000), supporting more and higher trophic levels and thus larger top predators in large lakes. Additionally, fish in large lakes might be less vulnerable to fisheries (Wilde & Pope 2004a) supporting a longer life span and consequently a larger maximum size.

Lake trophic status was an important predictor of variability in the size structure of lake fish assemblages at a small geographical scale (northern Germany, **paper IV**). However, across the large European scale (**paper V**) the trophic status explained almost no variability in the size structure of lake fish, although the large-scale dataset covered the full productivity gradient from ultra-oligotrophic to hypertrophic lakes. The lake trophic status is closely linked with lake depth and geographic location (Nõges 2009), which in turn determine lake temperature (Efremova & Palshin 2007). The small-scale study which only included lakes located in the Central Plains ecoregion (**paper IV**) was characterised by similar climatic conditions (*cf*. 3.2, Figure 5). Variability in the trophic status of lakes clearly affects the size structure of fish more strongly than the less pronounced climatic variability at this scale. By contrast, at a large geographical scale which covers subtropical to subpolar climates (**paper V**, Figure 6), lake temperature, characterised by the geographic location (elevation, latitude), was the main abiotic factor explaining variability in size structure between European lake fish assemblages. However, increases in nutrient concentration and temperature both had the same directional affect on the size structure of lake fish. Fish assemblages in nutrient-poor and in coldwater lakes were characterised by a higher relative proportion of large fish. Empirical evidence from recent studies indicates temperature as a more important factor than lake productivity to shape size structure of lake fish assemblages (Jeppesen et al. 2010; 2012). At comparable or even reduced nutrient concentrations, warmwater lakes exhibit higher fish densities (particularly for small-sized individuals) than coldwater lakes (Jeppesen et al. 2010). The results of **paper V** support the temperature-size rule which predicts a smaller body size for ectothermic animals at higher temperatures (Atkinson 1994).

Biotic variables, especially those relating to the functional classification of fish into feeding guilds (**paper IV**) and thermal guilds (**paper V**) were found to play an important role in the study lakes. High predator abundances resulted in a greater number of large fish in an assemblage, and a dominance of small-sized and medium-sized fish was observed at high predator biomasses and in situations of small predator-prey-length ratios. This suggests a limited regulatory impact of predators on their prey in the northern German lakes (*cf*. Mehner 2010). Species shifts along distinct elevation and latitudinal gradients generated two types of fish assemblages in European lakes which fundamentally

differed in their size structure (**paper V**). The size structure of lowland lake fish assemblages dominated by eurythermic coolwater and/or eurythermic warmwater fish (mainly percids and cyprinids) differed substantially from the size structure of fish assemblages dominated by stenothermic coldwater fish (salmonids) which primarily populate lakes at higher-elevation sites in northern and southern Europe. The major shift in size structure of lake fish assemblages with increasing elevation and decreasing temperature was accompanied by a switch in the dominant life-history strategy from a periodic strategy of fish in cool- and warmwater lakes to more of an equilibrium life-history strategy of fish populating coldwater lakes (*cf*. Winemiller & Rose 1992; Vila-Gispert & Moreno-Amich 2002). The periodic life-history strategy is characteristic for fish such as perch and roach which mature early, have a low fecundity and a small adult size (Vila-Gispert & Moreno-Amich 2002). By contrast, larger-sized salmonids such as brown trout and charr, classified as species with a life-history strategy closer to the equilibrium type (Winemiller & Rose 1992) mature later, have a higher fecundity and a larger adult size.

The population size structure of coolwater perch and warmwater roach (and other warmwater fish) were similar and typically dominated by small-sized individuals. However, they fundamentally differed from the population size structure of coldwater salmonids which were typically dominated by larger-sized fish. Accordingly, a switch from cyprinid- and/or percid-dominated assemblages to salmonid-dominated assemblages is accompanied by a strong shift in size structure towards larger fish in salmonid-dominated systems. This suggests that fish assemblages dominated by coolwater and/or warmwater species are relatively robust against environmental modifications and a shift in the relative abundance of coolwater and warmwater fish will not likely result in a strong shift in their size structure. In contrast, coldwater fish assemblages at higher elevation lakes may suffer dramatic consequences from global warming, for instance, as predicted species shifts towards more eurythermic species (Reist et al. 2006; Heino et al. 2009; Jeppesen et al. 2010) are likely to be accompanied by substantial shifts in assemblage size structure. The empirical findings of the large-scale study (**paper V**) can be relevant to predict changes in the size structure of European lake fish assemblages to future climate change. How shifts in the size structure affect ecosystem organisation is an important topic for future research (Parmesan 2006; Dossena et al. 2012)

6 Conclusions

Non-standardised catch data from rod-and-reel recreational angling are of limited quality for the characterisation of, and comparison between fish stocks across a series of lakes. The reliability of the data will strongly depend upon which angler type is reporting the data. Vertical downward-looking

hydroacoustics is an adequate and efficient method for the quantification of fish biomass in stratified lakes. Survey designs combining hydroacoustics and limited gillnetting at sampling dates with short time intervals, the latter for inventory sampling only (*i.e*. collecting ground-truth information for the apportionment of species data to hydroacoustic data) rather than CPUE calculations, are a cost-effective strategy for sampling lake fish assemblages. Trawling should be more frequently applied in very large and deep lakes, and in lakes with large pelagic fish stocks to quantify pelagic fish biomass and/or to aid with the interpretation of hydroacoustic data as a source of ground-truth information.

Non-taxonomic size metrics calculated from fish catches in standardised multi-mesh gillnets can be used to identify systematic variations in the size structure of European lake fish assemblages along abiotic and biotic gradients at both small and large geographical scales. Lake morphometry and lake productivity together with the size and abundances of piscivorous fish determine lake fish assemblage size structure at small geographical scales. Differences in the environmental temperature of the fish, described by elevation and latitude of the lake in which fish was caught had the largest influence on differences in the size structure at a large geographical scale. Fish assemblages of lowland lakes which are dominated by coolwater and/or warmwater species are relatively robust against environmental modifications and a shift in the relative abundance of coolwater and warmwater fish will not likely result in a strong shift in their size structure. Fish assemblages in coldwater lakes which are typically dominated by larger-sized salmonids are likely subjected to substantial shifts in the size structure towards more small-sized individuals in consequence of future global warming. These empirical findings may support predictions of the response of lake fish assemblage structure to future anthropogenic disturbances and environmental changes.

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References

Achleitner, D., H. Gassner, and M. Luger. 2012. Comparison of three standardised fish sampling methods in 14 alpine lakes in Austria. Fisheries Management and Ecology **19**:352–361.

Alós, J., R. Arlinghaus, M. Palmer, D. March, and I. Álvarez. 2009. The influence of type of natural bait on fish catches and hooking location in a mixed-species marine recreational fishery, with implications for management. Fisheries Research **97**:270–277.

Amundsen, P.A. 1988. Effects of an intensive fishing programme on age structure, growth and parasite infection of stunted whitefish (*Coregonus lavaretus* L. s.l.) in Lake Stuorajavri, northern Norway. Finnish Fisheries Research **9**: 425–434.

Ansari, A. A., S. S. Gill, and F. A. Khan. 2011. Eutrophication: threat to aquatic ecosystems. Pages 143–170 in A. A., Ansari, S., Singh Gill, G. R., Lanza, and W., Rast, editors. Eutrophication: causes, consequences and control. Springer, Dordrecht, Netherlands.

Appelberg, M., H. M. Berger, T. Hesthagen, E. Kleiven, M. Kurkilahti, J. Raitaniemi, and M. Rask. 1995. Development and intercalibration of methods in Nordic freshwater fish monitoring. Water Air and Soil Pollution **85**:401–406.

Appenzeller, A. R., and W. C. Leggett. 1992. Bias in hydroacoustic estimates of fish abundance due to acoustic shadowing - evidence from day night surveys of vertically migrating fish. Canadian Journal of Fisheries and Aquatic Sciences **49**:2179–2189.

Arlinghaus, R., T. Klefoth, A. Kobler, and S. J. Cooke. 2008. Size selectivity, injury, handling time, and determinants of initial hooking mortality in recreational angling for northern pike: the influence of type and size of bait. North American Journal of Fisheries Management **28**:123–134.

Arlinghaus, R., and T. Mehner. 2003. Socio-economic characterisation of specialised common carp (*Cyprinus carpio* L.) anglers in Germany, and implications for inland fisheries management and eutrophication control. Fisheries Research **61**:19–33.

Arlinghaus, R., and T. Mehner. 2004. A management-orientated comparative analysis of urban and rural anglers living in a metropolis (Berlin, Germany). Environmental Management **33**:331–344.

Atkinson, D. 1994. Temperature and organism size - a biological law for ectotherms? Advances in Ecological Research **25**:1–58.

Atkinson, D., and R. M. Sibly. 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. Trends in Ecology & Evolution **12**:235–239.

Balk, H., and T. Lindem. 2007. Sonar4 and Sonar5-Pro post processing systems. Operator manual, Version 5.9.7. Balk and Lindem Data Acquisition, Oslo, Norway.

Balk, H., and T. Lindem. 2011. Sonar4 and Sonar5-Pro post processing systems. Operator manual version 6.01, Balk and Lindem Data Acquisition, Oslo, Norway.

Beardmore, B., W. Haider, L. M. Hunt, and R. Arlinghaus. 2011. The importance of trip context for determining primary angler motivations: are more specialized anglers more catch-oriented than previously believed? North American Journal of Fisheries Management **31**:861–879.

Beier, U. 2001. Habitat distribution and size structure in freshwater fish communities: effects of vendace on interactions between perch and roach. Journal of Fish Biology **59**:1437–1454.

Beukema, J. J. 1970. Acquired hook-avoidance in the pike *Esox lucius* L. fished with artificial and natural baits. Journal of Fish Biology **2**:155–160.

Blanck, A., and N. Lamouroux. 2007. Large-scale intraspecific variation in life-history traits of European freshwater fish. Journal of Biogeography **34**:862–875.

Blueweiss, L., H. Fox, V. Kudzma, D. Nakashima, R. Peters, and S. Sams. 1978. Relationships between body size and some life history parameters. Oecologia **37**:257–272.

Blumenshine, S. C., D. M. Lodge, and J. R. Hodgson. 2000. Gradient of fish predation alters body size distributions of lake benthos. Ecology **81**:374–386.

Bobori, D. C., and I. Salvarina. 2010. Seasonal variation of fish abundance and biomass in gillnet catches of an East Mediterranean lake: Lake Doirani. Journal of Environmental Biology **31**:995–1000.

Bonar, S. A., and W. A. Hubert. 2002. Standard sampling of inland fish: benefits, challenges, and a call for action. Fisheries **27**:10–16.

Bonar, S. A., W. A. Hubert, and D. W. Willis. 2009. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, USA.

Borcard, D., P. Legendre, C. Avois-Jacquet, and H. Tuomisto. 2004. Dissecting the spatial structure of ecological data at multiple scales. Ecology **85**:1826–1832.

Brämick, U., M. Diekmann, R. Lemcke, and T. Mehner. 2008. Assessing shifts in fish assemblages of German large lakes by literature data and commercial catch statistics. Fundamental and Applied Limnology **171**:87–103.

Brämick, U., and R. Lemcke. 2003. Regional application of a fish yield estimation procedure to lakes in north-east Germany. Limnologica - Ecology and Management of Inland Waters **33**:205–213.

Bray, G. S., and H. L. Schramm. 2001. Evaluation of a statewide volunteer angler diary program for use as a fishery assessment tool. North American Journal of Fisheries Management **21**:606–615.

Brönmark, C., C. A. Paszkowski, W. M. Tonn, and A. Hargeby. 1995. Predation as a determinant of size structure in populations of crucian carp (*Carassius carassius*) and tench (*Tinca tinca*). Ecology of Freshwater Fish **4**:85–92.

Brooks, J. L., and S. I. Dodson. 1965. Predation body size and composition of plankton. Science **150**:28–35.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology **85**:1771–1789.

Brylinsky, M., and K. H. Mann. 1973. An analysis of factors governing productivity in lakes and reservoirs. Limnology and Oceanography **18**:1–14.

Buchanan, S., A. P. Farrell, J. Fraser, P. Gallaugher, R. Joy, and R. Routledge. 2002. Reducing gill-net mortality of incidentally caught coho salmon. North American Journal of Fisheries Management **22**:1270–1275.

Burrough, R. J., and C. R. Kennedy. 1979. The occurrence and natural alleviation of stunting in a population of roach, *Rutilus rutilus* (L.). Journal of Fish Biology **15**:93–109.

Byström, P. 2006. Recruitment pulses induce cannibalistic giants in Arctic char. Journal of Animal Ecology **75**:434–444.

Calder, W.A. 1984. Size function and life history. Harvard University Press, Cambridge, UK.

Carpenter, S. R., D. Bolgrien, R. C. Lathrop, C. A. Stow, T. Reed, and M. A. Wilson. 1998. Ecological and economic analysis of lake eutrophication by nonpoint pollution. Australian Journal of Ecology **23**:68–79.

Carpenter, S. R., and J. F. Kitchell. 1996. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Caussé, S., M. Gevrey, S. Pédron, S. Brucet, K. Holmgren, M. Emmrich, J. De Bortoli, and C. Argillier. 2011. Fish indicators for ecological status assessment of lakes affected by eutrophication and hydromorphological pressures. WISER Deliverable 3.4-4, European Commission.

Cazemier, W. G. 1982. The growth of bream (*Abramis brama* L.) in relation to habitat and population density. Hydrobiological Bulletin **16**:269–277.

CEN (European Committee for Standardization). 2005. EN 14757. Water quality - Sampling of fish with multi-mesh gill nets. Brussels, Belgium.

CEN (European Committee for Standardization). 2009. prEN 15910. Water quality - Guidance on the estimation of fish abundance with mobile hydroacoustic methods. Brussels, Belgium.

Claessen, D., A. M. De Roos, and L. Persson. 2000. Dwarfs and giants: Cannibalism and competition in size-structured populations. American Naturalist **155**:219–237.

Claessen, D., C. Van Oss, A. M. De Roos, and L. Persson. 2002. The impact of size-dependent predation on population dynamics and individual life history. Ecology **83**:1660–1675.

Cooper, M. J., and G. A. Wheatley. 1981. An examination of the fish population in the River Trent, Nottinghamshire using angler catches. Journal of Fish Biology **19**:539–556.

Dahm, E., J. Hartmann, J. Jurvelius, H. Löffler, and V. Völzke. 1992. Review of the European-Inland-Fisheries-Advisory-Commission (EIFAC) experiments on stock assessment in lakes. Journal of Applied Ichthyology **8**:1–9.

Damuth, J. D. 1992. Taxon-free characterization of animal communities. Pages 183–203 in Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, J., and S.L., Wing editors. Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals. University of Chicago Press, Chicago, USA.

Daniel, T. C., A. N. Sharpley, and J. L. Lemunyon. 1998. Agricultural phosphorus and eutrophication: a symposium overview. Journal of Environmental Quality **27**:251–257.

Daufresne, M., K. Lengfellner, and U. Sommer. 2009. Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences **106**:12788–12793.

De Eyto, E., and K. Irvine. 2007. Assessing the status of shallow lakes using an additive model of biomass size spectra. Aquatic Conservation-Marine and Freshwater Ecosystems **17**:724–736.

De Leeuw, J. J., L. A. J. Nagelkerke, W. L. T. Van Densen, K. Holmgren, P. A. Jansen, and J. Vijverberg. 2003. Biomass size distributions as a tool for characterizing lake fish communities. Journal of Fish Biology **63**:1454–1475.

Deceliere-Vergès, C., C. Argillier, C. Lanoiselée, J. De Bortoli, and J. Guillard. 2009. Stability and precision of the fish metrics obtained using CEN multi-mesh gillnets in natural and artificial lakes in France. Fisheries Research **99**:17–25.

Deceliere-Vergès, C., and J. Guillard. 2008. Assessment of the pelagic fish populations using CEN multi-mesh gillnets: consequences for the characterization of the fish communities. Knowledge and Management of Aquatic Ecosystems **389**:04.

Declerck, S. A. J., J. S. Coronel, P. Legendre, and L. Brendonck. 2011. Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. Ecography **34**:296–305.

Deelder, C.L. 1951. A contribution to the knowledge of the stunted growth of perch (*Perca fluviatilis* L.) in Holland. Hydrobiologia **3**:357–378.

Degerman, E., P. Nyberg, and M. Appelberg. 1988. Estimating the number of species and relative abundance of fish in oligotrophic Swedish lakes using multi-mesh gill nets. Nordic Journal of Freshwater Research **64**:91–100.

Dennerline, D. E., C. A. Jennings, and D. J. Degan. 2012. Relationships between hydroacoustic derived density and gill net catch: Implications for fish assessments. Fisheries Research **123–124**:78–89.

Diehl, S. 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. Oikos **53**:207–214.

Doi, H., K.-H. Chang, T. Ando, H. Imai, and S. Nakano. 2010. Shoreline bank construction modifies benthic–pelagic coupling of food webs. Ecological Engineering **36**:601–604.

Dörner, H., S. Hülsmann, F. Hölker, C. Skov, and A. Wagner. 2007. Size-dependent predator-prey relationships between pikeperch and their prey fish. Ecology of Freshwater Fish **16**:307–314.

Dörner, H., and A. Wagner. 2003. Size-dependent predator-prey relationships between perch and their fish prey. Journal of Fish Biology **62**:1021–1032.

Dörner, H., A. Wagner, and J. Benndorf. 1999. Predation by piscivorous fish on age-0 fish: spatial and temporal variability in a biomanipulated lake (Bautzen reservoir, Germany). Hydrobiologia **408-409**:39–46.

Dorow, M., and R. Arlinghaus. 2011. A telephone-diary-mail approach to survey recreational fisheries on large geographic scales, with a note on annual landings estimates by anglers in northern Germany. Pages 319–344 in J.D., Beard, R., Arlinghaus, and S.G., Sutton editors. The angler in the environment: social, economic, biological and ethical dimensions. Proceedings from the

fifth world recreational fishing conference. American Fisheries Society Symposium **75**. Bethesda, USA.

Dossena, M., G. Yvon-Durocher, J. Grey, J. M. Montoya, D. M. Perkins, M. Trimmer, and G. Woodward. 2012. Warming alters community size structure and ecosystem functioning. Proceedings of the Royal Society B: Biological Sciences **279**:3011–3019.

Downing, J. A., C. Plante, and S. Lalonde. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Canadian Journal of Fisheries and Aquatic Sciences **47**:1929–1936.

Draštík, V. et al. 2009. Hydroacoustic estimates of fish stocks in temperate reservoirs: day or night surveys? Aquatic Living Resources **22**:69–77.

Draštík, V., and J. Kubečka. 2005. Fish avoidance of acoustic survey boat in shallow waters. Fisheries Research **72**:219–228.

Eaton, J. G., and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. Limnology and Oceanography **41**:1109–1115.

Eckmann, R., S. Gerster, and A. Kraemer. 2006. Yields of European perch from upper Lake Constance from 1910 to present. Fisheries Management and Ecology **13**:381–390.

Edmundson, J. A., and A. Mazumder. 2002. Regional and hierarchical perspectives of thermal regimes in subarctic, Alaskan lakes. Freshwater Biology **47**:1–17.

Efremova, T., and N. Palshin. 2007. Effect of climate and morphometry on thermal regime of lakes. 16th international northern research basins symposium and workshop, 36–44. Petrozavodsk, Russia.

Elliott, J. M., and J. M. Fletcher. 2001. A comparison of three methods for assessing the abundance of Arctic charr, *Salvelinus alpinus*, in Windermere (northwest England). Fisheries Research **53**:39–46.

Emmrich, M., S. Brucet, I.J. Winfield, E. Jeppesen, T.L. Lauridsen, P. Volta, C. Argillier, S. Pédron, K. Holmgren, T. Hesthagen, D. Ritterbusch, and T. Mehner. 2011. Changes in size structure of fish assemblages in European lakes along eutrophication and hydromorphological pressure gradients. WISER Deliverable 3.4-2, European Commission.

Elton, C. S. 1927. Animal ecology. Macmillan, New York, USA.

Emmerson, M. C., and D. Raffaelli. 2004. Predator-prey body size, interaction strength and the stability of a real food web. Journal of Animal Ecology **73**:399–409.

European Communities. 1992. Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora. Official Journal of the European Communities **L 206**:7–50.

European Union. 2000. Directive 2000/60EC of the European Parliament and of the Council of Establishment a framework of the community action in the field of water policy. European Commission. Official Journal of the European Communities, **L327:**1.

Finstad, A. G., P. A. Jansen, and A. Langeland. 2000. Gillnet selectivity and size and age structure of an alpine Arctic char (*Salvelinus alpinus*) population. Canadian Journal of Fisheries and Aquatic Sciences **57**:1718–1727.

Gabriel, O., K. Lange, E. Dahm, and T. Wendt. 2005. Fish catching methods of the world. John Wiley & Sons, Oxford, UK.

Gaedke, U. 1992. The size distribution of plankton biomass in a large lake and its seasonal variability. Limnology and Oceanography **37**:1202–1220.

Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: a third universal response to warming? Trends in Ecology & Evolution **26**:285–291.

Gassner, H., G. Tischler, and J. Wanzenböck. 2003. Ecological integrity assessment of lakes using fish communities - Suggestions of new metrics developed in two Austrian prealpine lakes. International Review of Hydrobiology **88**:635–652.

Gassner, H., J. Wanzenböck, D. Zick, G. Tischler, and B. Pamminger-Lahnsteiner. 2005. Development of a fish based lake typology for natural Austrian lakes > 50 ha based on the reconstructed historical fish communities. International Review of Hydrobiology **90**:422–432.

Gerdeaux, D., and M. Y. Janjua. 2009. Contribution of obligatory and voluntary fisheries statistics to the knowledge of whitefish population in Lake Annecy (France). Fisheries Research **96**:6–10.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology **65**:455–468.

Godlewska, M., M. Colon, L. Doroszczyk, B. Długoszewski, C. Verges, and J. Guillard. 2009. Hydroacoustic measurements at two frequencies: 70 and 120 kHz - consequences for fish stock estimation. Fisheries Research **96**:11–16.

Godlewska, M., M. Colon, A. Jóźwik, and J. Guillard. 2011. How pulse lengths impact fish stock estimations during hydroacoustic measurements at 70 kHz. Aquatic Living Resources **24**:71–78.

Godlewska, M., and A. Świerzowski. 2003. Hydroacoustical parameters of fish in reservoirs with contrasting levels of eutrophication. Aquatic Living Resources **16**:167–173.

Godlewska, M., A. Świerzowski, and I. J. Winfield. 2004. Hydroacoustics as a tool for studies of fish and their habitat. Ecohydrology & Hydrobiology **4**:417–427.

Greene, C. H. 1983. Selective predation in freshwater zooplankton communities. Internationale Revue der gesamten Hydrobiologie und Hydrographie **68**:297–315.

Griffiths, D. 2012. Body size distributions in North American freshwater fish: large-scale factors. Global Ecology and Biogeography **21**:383–392.

Guillard, J., P. Balay, M. Colon, and P. Brehmer. 2010. Survey boat effect on YOY fish schools in a pre-alpine lake: evidence from multibeam sonar and split-beam echosounder data. Ecology of Freshwater Fish **19**:373–380.

Guillard, J., A. Lebourges-Dhaussy, and P. Brehmer. 2004. Simultaneous Sv and TS measurements on Young-of-the-Year (YOY) freshwater fish using three frequencies. ICES Journal of Marine Science **61**:267–273.

Gulland, J. A. 1980. General concepts of sampling fish. EIFAC (European Inland Fisheries Advisory Commission) Technical Paper **33**:7–12.

Haakana, H., and H. Huuskonen. 2008. Effects of intensive fishing on the perch population in a large oligotrophic lake in eastern Finland. Fisheries Research **91**:144–150.

Hamley, J. M. 1975. Review of gillnet selectivity. Journal of the Fisheries Research Board of Canada **32**:1943–1969.

Hanson, J. M., and W. C. Leggett. 1982. Empirical prediction of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Sciences **39**:257–263.

Harper, D. 1992. Eutrophication of freshwaters: principles, problems and restoration. Chapman and Hall, London, UK.

Harrison, A. J., F. L. Kelly, R. S. Rosell, T. W. S. Champ, L. Connor, and J. R. Girvan. 2010. First record and initial hydroacoustic stock assessment of Pollan *Coregonus autumnalis* PALLAS in Lough Allen, Ireland. Biology & Environment: Proceedings of the Royal Irish Academy **110**:69–74.

He, P., and M. Pol. 2010. Fish behavior near gillnets: capture processes, and influencing factors. Pages 183–203 in P. He, editor. Behavior of marine fishes. Wiley-Blackwell, Oxford, UK.

Heath, D. D., and D. A. Roff. 1996. The role of trophic bottlenecks in stunting: A field test of an allocation model of growth and reproduction in yellow perch, *Perca flavescens*. Environmental Biology of Fishes **45**:53–63.

Heibo, E., C. Magnhagen, and L. A. Vøllestad. 2005. Latitudinal variation in life-history traits in Eurasian perch. Ecology **86**:3377–3386.

Heino, J., T. Eros, J. Kotanen, and M. Rask. 2010. Describing lake fish communities: Do presence-absence and biomass data show similar spatial and environmental relationships? Boreal Environment Research **15**:69–80.

Heino, J., R. Virkkala, and H. Toivonen. 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. Biological Reviews **84**:39–54.

Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. Journal of the Fisheries Research Board of Canada **34**:1524–1550.

Holmgren, K., and M. Appelberg. 2000. Size structure of benthic freshwater fish communities in relation to environmental gradients. Journal of Fish Biology **57**:1312–1330.

Holmgren, K., and M. Appelberg. 2001. Effects of environmental factors on size-related growth efficiency of perch, Perca fluviatilis. Ecology of Freshwater Fish **10**:247–256.

Illies, J. 1978. Limnofauna Europaea. Gustav Fischer, Stuttgart, Germany.

Imbrock, F., A. Appenzeller, and R. Eckmann. 1996. Diel and seasonal distribution of perch in Lake Constance: A hydroacoustic study and in situ observations. Journal of Fish Biology **49**:1–13.

Jackson, D. A., and H. H. Harvey. 1989. Biogeographic associations in fish assemblages: local vs regional processes. Ecology **70**:1472–1484.

Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences **58**:157–170.

Janhunen, M., N. Peuhkuri, and J. Piironen. 2010. A comparison of growth patterns between a stunted and two large predatory Arctic charr populations under identical hatchery conditions. Environmental Biology of Fishes **87**:113–121.

Jennings, M. J., M. A. Bozek, G. R. Hatzenbeler, E. E. Emmons, and M. D. Staggs. 1999. Cumulative effects of incremental shoreline habitat modification on fish assemblages in north temperate lakes. North American Journal of Fisheries Management **19**:18–27.

Jennings, S., J. K. Pinnegar, N. V. C. Polunin, and T. W. Boon. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. Journal of Animal Ecology **70**:934–944.

Jennings, S., and K. J. Warr. 2003. Smaller predator-prey body size ratios in longer food chains. Proceedings of the Royal Society of London Series B-Biological Sciences **270**:1413–1417.

Jeppesen, E. et al. 2010. Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. Hydrobiologia **646**:73–90.

Jeppesen, E. et al. 2012. Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. Hydrobiologia:1–39.

Jeppesen, E., J. P. Jensen, C. Jensen, B. Faafeng, D. O. Hessen, M. Søndergaard, T. Lauridsen, P. Brettum, and K. Christoffersen. 2003. The impact of nutrient state and lake depth on top-down control in the pelagic zone of lakes: A study of 466 lakes from the temperate zone to the arctic. Ecosystems **6**:313–325.

Jeppesen, E., J. P. Jensen, M. Søndergaard, T. Lauridsen, and F. Landkildehus. 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshwater Biology **45**:201–218.

Jeppesen, E., J. P. Jensen, M. Søndergaard, T. Lauridsen, L. J. Pedersen, and L. Jensen. 1997. Top-down control in freshwater lakes: The role of nutrient state, submerged macrophytes and water depth. Hydrobiologia **342**:151–164.

Jeppesen, E., Z. Pekcan-Hekim, T. L. Lauridsen, M. Søndergaard, and J. P. Jensen. 2006. Habitat distribution of fish in late summer: changes along a nutrient gradient in Danish lakes. Ecology of Freshwater Fish **15**:180–190.

Johnston, I. A., and A. F. Bennett. 1996. Animals and temperature. Cambridge University Press, Cambridge, UK.

Jurvelius, J., H. Auvinen, I. Kolari, and T. J. Marjomäki. 2005. Density and biomass of smelt (*Osmerus eperlanus*) in five Finnish lakes. Fisheries Research **73**:353–361.

Jurvelius, J., I. Kolari, and A. Leskelä. 2011. Quality and status of fish stocks in lakes: gillnetting, seining, trawling and hydroacoustics as sampling methods. Hydrobiologia **660**:29–36.

Jurvelius, J., R. Riikonen, T. J. Marjomäki, and J. Lilja. 2000. Mortality of pike-perch (*Stizostedion lucioperca*), brown trout (*Salmo trutta*) and landlocked salmon (*Salmo salar* m. *sebago*) caught as by-catch in pelagic trawling in a Finnish lake. Fisheries Research **45**:291–296.

Jurvelius, J., and I. Sammalkorpi. 1995. Hydroacoustic monitoring of the distribution, density and the mass-removal of pelagic fish in a eutrophic lake. Hydrobiologia **316**:33–41.

Kekäläinen, J., J. Kähkönen, V. Kiviniemi, and H. Huuskonen. 2010. Morphological variation of perch *Perca fluviatilis* in humic lakes: the effect of predator density, competition and prey abundance. Journal of Fish Biology **76**:787–799.

Kerr, S.R., and L.M. Dickie. 2001. The biomass spectrum: A predator-prey theory of aquatic production. Columbia University Press, New York, USA.

Knouft, J. H. 2004. Latitudinal variation in the shape of the species body size distribution: an analysis using freshwater fishes. Oecologia **139**:408–417.

Kottelat, M., and J. Freyhof. 2007. Handbook of European freshwater fishes. Publications Kottelat, Cornol, Switzerland.

Kubečka, J. et al. 2009. The true picture of a lake or reservoir fish stock: A review of needs and progress. Fisheries Research **96**:1–5.

Kubečka, J., O. R. Godø, P. Hickley, M. Prchalová, M. Říha, L. Rudstam, and R. Welcomme. 2012. Fish sampling with active methods. Fisheries Research **123–124**:1–3.

Kuparinen, A., T. Klefoth, and R. Arlinghaus. 2010. Abiotic and fishing-related correlates of angling catch rates in pike (*Esox lucius*). Fisheries Research **105**:111–117.

Kurkilahti, M., M. Appelberg, E. Bergstrand, and O. Enderlein. 1998. An indirect estimate of bimodal gillnet selectivity of smelt. Journal of Fish Biology **52**:243–254.

Kurkilahti, M., and M. Rask. 1996. A comparative study of the usefulness and catchability of multimesh gill nets and gill net series in sampling of perch (*Perca fluviatilis* L) and roach (*Rutilus rutilus* L). Fisheries Research **27**:243–260.

Lappalainen, J., A. S. Tarkan, and C. Harrod. 2008. A meta-analysis of latitudinal variations in life-history traits of roach, *Rutilus rutilus*, over its geographical range: linear or non-linear relationships? Freshwater Biology **53**:1491–1501.

Lauridsen, T. L., F. Landkildehus, E. Jeppesen, T. B. Jorgensen, and M. Søndergaard. 2008. A comparison of methods for calculating Catch Per Unit Effort (CPUE) of gill net catches in lakes. Fisheries Research **93**:204–211.

Lehtonen, H. 1996. Potential effects of global warming on northern European freshwater fish and fisheries. Fisheries Management and Ecology **3**:59–71.

Lewin, W., N. Okun, and T. Mehner. 2004. Determinants of the distribution of juvenile fish in the littoral area of a shallow lake. Freshwater Biology **49**:410–424.

Lewin, W.-C., R. Arlinghaus, and T. Mehner. 2006. Documented and potential biological impacts of recreational fishing: Insights for management and conservation. Reviews in Fisheries Science **14**:305–367.

Lindsey, C. C. 1966. Body sizes of poikilotherm vertebrates at different latitudes. Evolution **20**:456–465.

Linfield, R. S. J. 1980. Ecological changes in a lake fishery and their effects on a stunted roach *Rutilus rutilus* population. Journal of Fish Biology **16**:123–144.

Linløkken, A., and T. O. Haugen. 2006. Density and temperature dependence of gill net catch per unit effort for perch, *Perca fluviatilis*, and roach, *Rutilus rutilus*. Fisheries Management and Ecology **13**:261–269.

Linløkken, A., H. Seeland, and P. Arne. 1996. Growth and production of perch (*Perca fluviatilis* L.) responding to biomass removal. Annales Zoologici Fennici **33**:427–435.

Lux, F. E., and L. L. Smith. 1960. Some factors influencing seasonal changes in angler catch in a Minnesota lake. Transactions of the American Fisheries Society **89**:67–79.

Macbeth, W. G., M. K. Broadhurst, B. D. Paterson, and M. E. L. Wooden. 2006. Reducing the short-term mortality of juvenile school prawns (*Metapenaeus macleayi*) discarded during trawling. ICES Journal of Marine Science **63**:831–839.

Magnuson, J. J., L. B. Crowder, and P. A. Medvick. 1979. Temperature as an ecological resource. American Zoologist **19**:331–343.

Mason, C. F. 2002. Biology of freshwater pollution. Longman, London, UK.

Mason, D. M. et al. 2005. Hydroacoustic estimates of abundance and spatial distribution of pelagic prey fishes in western Lake Superior. Journal of Great Lakes Research **31**:426–438.

McClatchie, S., R. E. Thorne, P. Grimes, and S. Hanchet. 2000. Ground truth and target identification for fisheries acoustics. Fisheries Research **47**:173–191.

McConnell, K. E., I. E. Strand, and L. Blake-Hedges. 1995. Random utility models of recreational fishing: Catching fish using a poisson process. Marine Resource Economics **10**:247–261.

Mcdonald, M. E., and A. E. Hershey. 1989. Size structure of a lake trout (*Salvelinus namaycush*) population in an arctic lake - Influence of angling and implications for fish community structure. Canadian Journal of Fisheries and Aquatic Sciences **46**:2153–2156.

Mehner, T. 2010. No empirical evidence for community-wide top-down control of prey fish density and size by fish predators in lakes. Limnology and Oceanography **55**:203–213.

Mehner, T., M. Diekmann, U. Brämick, and R. Lemcke. 2005. Composition of fish communities in German lakes as related to lake morphology, trophic state, shore structure and human-use intensity. Freshwater Biology **50**:70–85.

Mehner, T., K. Holmgren, T. L. Lauridsen, E. Jeppesen, and M. Diekmann. 2007. Lake depth and geographical position modify lake fish assemblages of the European 'Central Plains' ecoregion. Freshwater Biology **52**:2285–2297.

Mehner, T., and M. Schulz. 2002. Monthly variability of hydroacoustic fish stock estimates in a deep lake and its correlation to gillnet catches. Journal of Fish Biology **61**:1109–1121.

Mosindy, T., and M. Duffy. 2007. The use of angler diary surveys to evaluate long-term changes in muskellunge populations on Lake of the Woods, Ontario. Pages 71–83 in J. S., Diana, T. L., Margenau, and D. L. G., Noakes, editors. The muskellunge symposium: a memorial tribute to E.J. Crossman. Developments in Environmental Biology of Fishes **26**. Springer, Dordrecht, Netherlands.

Mosindy, T. E., W. T. Momot, and P. J. Colby. 1987. Impact of angling on the production and yield of mature walleyes and northern pike in a small boreal lake in Ontario. North American Journal of Fisheries Management **7**:493–501.

Mous, P. J., W. L. T. van Densen, and M. A. M. Machiels. 2002. The effect of smaller mesh sizes on catching larger fish with trawls. Fisheries Research **54**:171–179.

Murawski, S. A., and J. S. Idoine. 1992. Multispecies size composition: A conservative property of exploited fishery systems? Journal of Northwest Atlantic Fishery Science **14**:79–85.

Nilsson, P. A., and C. Brönmark. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. Oikos **88**:539–546.

Nõges, T. 2009. Relationships between morphometry, geographic location and water quality parameters of European lakes. Hydrobiologia **633**:33–43.

Northcote, T. G. 1988. Fish in the structure and function of freshwater ecosystems: A 'top-down' view. Canadian Journal of Fisheries and Aquatic Sciences **45**:361–379.

Olin, M., M. Kurkilahti, P. Peitola, and J. Ruuhijärvi. 2004. The effects of fish accumulation on the catchability of multimesh gillnet. Fisheries Research **68**:135–147.

Olin, M., I. Malinen, and J. Ruuhijärvi. 2009. Gillnet catch in estimating the density and structure of fish community - Comparison of gillnet and trawl samples in a eutrophic lake. Fisheries Research **96**:88–94.

Olin, M., and T. Malinen. 2003. Comparison of gillnet and trawl in diurnal fish community sampling. Hydrobiologia **506**:443–449.

Olin, M., M. Rask, J. Ruuhijärvi, M. Kurkilahti, P. Ala-Opas, and O. Ylonen. 2002. Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. Journal of Fish Biology **60**:593–612.

Olin, M., M. Vinni, H. Lehtonen, M. Rask, J. Ruuhijärvi, K. Saulamo, and P. Ala-Opas. 2010. Environmental factors regulate the effects of roach *Rutilus rutilus* and pike *Esox lucius* on perch *Perca fluviatilis* populations in small boreal forest lakes. Journal of Fish Biology **76**:1277–1293.

Olson, M. H. 1996. Predator-prey interactions in size-structured fish communities: Implications of prey growth. Oecologia **108**:757–763.

Parker-Stetter, S. L., L. G. Rudstam, P. J. Sullivan, and D. M. Warner. 2009. Standard operating procedures for fisheries acoustic surveys in the Great Lakes. Great Lakes Fisheries Commission Special Publication 09-01. An Arbor, USA.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics **37**:637–669.

Peltonen, H., and J. Horppila. 1992. The effects of mass removal on the roach *Rutilus rutilus* (L.) stock of Lake Vesijärvi estimated with VPA within one season. Journal of Fish Biology **40**:293–301.

Peltonen, H., J. Ruuhijärvi, T. Malinen, and J. Horppila. 1999. Estimation of roach (*Rutilus rutilus* (L.)) and smelt (*Osmerus eperlanus* (L.)) stocks with virtual population analysis, hydroacoustics and gillnet CPUE. Fisheries Research **44**:25–36.

Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Canadian Journal of Fisheries and Aquatic Sciences **48**:503–518.

Persson, L. 1983. Food consumption and competition between age classes in a perch *Perca fluviatilis* population in a shallow eutrophic lake. Oikos **40**:197–207.

Persson, L., J. Andersson, E. Wahlström, and P. Eklöv. 1996. Size-specific interactions in lake systems: Predator gape limitation and prey growth rate and mortality. Ecology **77**:900–911.

Persson, L., S. Diehl, L. Johansson, G. Andersson, and S. F. Hamrin. 1991. Shifts in fish communities along the productivity gradient of femperate lakes - patterns and the importance of size-structured interactions. Journal of Fish Biology **38**:281–293.

Persson, L., A. M. D. Roos, D. Claessen, P. Byström, J. Lövgren, S. Sjögren, R. Svanbäck, E. Wahlström, and E. Westman. 2003. Gigantic cannibals driving a whole-lake trophic cascade. Proceedings of the National Academy of Sciences **100**:4035–4039.

Petchey, O. L., and A. Belgrano. 2010. Body-size distributions and size-spectra: universal indicators of ecological status? Biology Letters **6**:434–437.

Peters, R.H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, UK.

Pope, J.G., and B. J. Knights. 1982. Comparison of length distributions of combined catches of all demersal fishes in surveys in the North Sea and at Faroe Bank. Pages 116-118 in M.C., Mercer editor. Multispecies approaches to fisheries management advice. Canadian Special Publications in Fisheries and Aquatic Sciences **59**.

Portt, C. B., G. A. Coker, D. L. Ming, and R. G. Randall. 2006. A review of fish sampling methods commonly used in Canadian freshwater habitats. Canadian Technical Report of Fisheries and Aquatic Sciences **2604**.

Post, D. M., M. L. Pace, and N. G. Hairston. 2000. Ecosystem size determines food-chain length in lakes. Nature **405**:1047–1049.

Prchalová, M., J. Kubečka, M. Říha, R. Litvín, M. Čech, J. Frouzová, M. Hladík, E. Hohausova, J. Peterka, and M. Vašek. 2008. Overestimation of percid fishes (Percidae) in gillnet sampling. Fisheries Research **91**:79–87.

Prchalová, M., J. Kubečka, M. Říha, T. Mrkvička, M. Vašek, T. Jůza, M. Kratochvíl, J. Peterka, V. Draštík, and J. Křížek. 2009. Size selectivity of standardized multimesh gillnets in sampling coarse European species. Fisheries Research **96**:51–57.

Prchalová, M., T. Mrkvička, J. Kubečka, J. Peterka, M. Čech, M. Muška, M. Kratochvíl, and M. Vašek. 2010. Fish activity as determined by gillnet catch: A comparison of two reservoirs of different turbidity. Fisheries Research **102**:291–296.

Prchalová, M., T. Mrkvička, J. Peterka, M. Čech, L. Berec, and J. Kubečka. 2011. A model of gillnet catch in relation to the catchable biomass, saturation, soak time and sampling period. Fisheries Research **107**:201–209.

Prchalová, M., J. W. Neal, M. Muñoz-Hincapié, T. Jůza, M. Říha, J. Peterka, and J. Kubečka. 2012. Comparison of gill nets and fixed-frame trawls for sampling threadfin shad in tropical reservoirs. Transactions of the American Fisheries Society **141**:1151–1160.

Quintana, X. D., S. Brucet, D. Boix, R. López-flores, S. Gascón, A. Badosa, J. Sala, R. Moreno-Amich, and J. J. Egozcue. 2008. A nonparametric method for the measurement of size diversity with emphasis on data standardization. Limnology and Oceanography-Methods **6**:75–86.

Radke, R. J., and A. Gaupisch. 2005. Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian perch (*Perca fluviatilis*): possible implications for fish community structure in lakes. Naturwissenschaften **92**:91–94.

Rakowitz, G., M. Tušer, M. Říha, T. Jůza, H. Balk, and J. Kubečka. 2012. Use of high-frequency imaging sonar (DIDSON) to observe fish behaviour towards a surface trawl. Fisheries Research **123–124**:37–48.

Rawson, D. S. 1952. Mean depth and the fish production of large lakes. Ecology **33**:513–521.

Regier, H. A., and D. S. Robson. 1966. Selectivity of gill nets, especially to lake whitefish. Journal of the Fisheries Research Board of Canada **23**:423–454.

Reist, J. D., F. J. Wrona, T. D. Prowse, M. Power, J. B. Dempson, R. J. Beamish, J. R. King, T. J. Carmichael, and C. D. Sawatzky. 2006. General effects of climate change on arctic fishes and fish populations. AMBIO **35**:370–380.

Reuman, D. C., and J. E. Cohen. 2005. Estimating relative energy fluxes using the food web, species abundance, and body size. Advances In Ecological Research **36**:137–182.

Říha, M. et al. 2012. The size selectivity of the main body of a sampling pelagic pair trawl in freshwater reservoirs during the night. Fisheries Research **127–128**:56–60.

Rochet, M. J., and V. M. Trenkel. 2003. Which community indicators can measure the impact of fishing? A review and proposals. Canadian Journal of Fisheries and Aquatic Sciences **60**:86–99.

Rosenberger, A. E., and J. B. Dunham. 2005. Validation of abundance estimates from mark–recapture and removal techniques for rainbow trout captured by electrofishing in small streams. North American Journal of Fisheries Management **25**:1395–1410.

Ryder, R. A. 1965. A method for estimating potential fish production of north-temperate lakes. Transactions of the American Fisheries Society **94**:214–218.

Sahoo, G., and S. Schladow. 2008. Impacts of climate change on lakes and reservoirs dynamics and restoration policies. Sustainability Science **3**:189–199.

Scheuerell, M. D., and D. E. Schindler. 2004. Changes in the spatial distribution of fishes in lakes along a residential development gradient. Ecosystems **7**:98–106.

Schindler, D. E., S. I. Geib, and M. R. Williams. 2000. Patterns of fish growth along a residential development gradient in north temperate lakes. Ecosystems **3**:229–237.

Schmidt, M. B. 2009. Reactions of vendace (*Coregonus albula*, Linnaeus 1758) towards an approaching pelagic pair-trawl observed by split-beam echosounding. Fisheries Research **96**:95–101.

Schmidt, M. B., H. Gassner, and E. I. Meyer. 2005. Distribution and biomass of an underfished vendace, *Coregonus albula*, population in a mesotrophic German reservoir. Fisheries Management and Ecology **12**:169–175.

Schmidt-Kloiber, A., S. Moe, B. Dudley, J. Strackbein, and R. Vogl. 2012. The WISER metadatabase: the key to more than 100 ecological datasets from European rivers, lakes and coastal waters. Hydrobiologia. DOI: 10.1007/s10750-012-1295-6.

Sheldon, R. W., A. Prakash, and W. H. Sutcliff. 1972. Size distribution of particles in the ocean. Limnology and Oceanography **17**:327–340.

Sibly, R. M., and D. Atkinson. 1994. How rearing temperature affects optimal adult size in ectotherms. Functional Ecology **8**:486–493.

Simmonds, J., and D. MacLennan. 2005. Fisheries acoustics: Theory and practice, Second edition. Blackwell Publishing, Oxford, UK.

Smith, C., and P. Reay. 1991. Cannibalism in teleost fish. Reviews in Fish Biology and Fisheries **1**:41–64.

Smith, P. A. 2002. The relationship between stock and catch and the effect of bait on catch as determined for a UK recreational catch and release fishery. Fisheries Management and Ecology **9**:261–266.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: A review. Bulletin of Marine Science **60**:1129–1157.

Sprules, W. G., and M. Munawar. 1986. Plankton size spectra in relation to ecosystem productivity, size, and perturbation. Canadian Journal of Fisheries and Aquatic Sciences **43**:1789–1794.

Stockwell, J. D., D. L. Yule, T. R. Hrabik, J. V. Adams, O. T. Gorman, and B. V. Holbrook. 2007. Vertical distribution of fish biomass in lake superior: Implications for day bottom trawl surveys. North American Journal of Fisheries Management **27**:735–749.

Strayer, D. L., and S. E. G. Findlay. 2010. Ecology of freshwater shore zones. Aquatic Sciences **72**:127–163.

Suuronen, P., T. Turunen, M. Kiviniemi, and J. Karjalainen. 1995. Survival of vendace (*Coregonus albula*) escaping from a trawl cod end. Canadian Journal of Fisheries and Aquatic Sciences **52**:2527–2533.

Tammi, J., M. Appelberg, U. Beier, T. Hesthagen, A. Lappalainen, and M. Rask. 2003. Fish status survey of Nordic lakes: Effects of acidification, eutrophication and stocking activity on present fish species composition. Ambio **32**:98–105.

Teixeira-de Mello, F., M. Meerhoff, Z. Pekcan-Hekim, and E. Jeppesen. 2009. Substantial differences in littoral fish community structure and dynamics in subtropical and temperate shallow lakes. Freshwater Biology **54**:1202–1215.

Torgersen, T., and S. Kaartvedt. 2001. In situ swimming behaviour of individual mesopelagic fish studied by split-beam echo target tracking. ICES Journal of Marine Science **58**:346–354.

Vainikka, A., J. Koskimäki, P. T. Niemelä, and R. Kortet. 2012. Composition of the Eurasian perch (*Perca fluviatilis*) catches in ice fishing: Does capture order predict body size? Fisheries Research **115–116**:24–30.

Van Den Avyle, M. J., J. Boxrucker, P. Michaletz, B. Vondracek, and G. R. Ploskey. 1995. Comparison of catch rate, length distribution, and precision of six gears used to sample reservoir shad populations. North American Journal of Fisheries Management **15**:940–955.

VanDeValk, A. J., J. L. Forney, J. R. Jackson, L. G. Rudstam, T. E. Brooking, and S. D. Krueger. 2005. Angler catch rates and catchability of walleyes in Oneida Lake, New York. North American Journal of Fisheries Management **25**:1441–1447.

Vašek, M., J. Kubečka, M. Čech, V. Draštík, J. Matěna, T. Mrkvička, J. Peterka, and M. Prchalová. 2009. Diel variation in gillnet catches and vertical distribution of pelagic fishes in a stratified European reservoir. Fisheries Research **96**:64–69.

Vidondo, B., Y. T. Prairie, J. M. Blanco, and C. M. Duarte. 1997. Some aspects of the analysis of size spectra in aquatic ecology. Limnology and Oceanography **42**:184–192.

Vijverberg, J., M. Boersma, W. L. T. Densen, W. Hoogenboezem, E. H. R. R. Lammens, and W. M. Mooij. 1990. Seasonal variation in the interactions between piscivorous fish, planktivorous fish and zooplankton in a shallow eutrophic lake. Hydrobiologia **207**:279–286.

Vila-Gispert, A., and R. Moreno-Amich. 2002. Life-history patterns of 25 species from European freshwater fish communities. Environmental Biology of Fishes **65**:387–400.

Vinni, M., J. Lappalainen, T. Malinen, and H. Lehtonen. 2009. Stunted growth of pikeperch *Sander lucioperca* in Lake Sahajärvi, Finland. Journal of Fish Biology **74**:967–972.

Volta, P., A. Oggioni, R. Bettinetti, and E. Jeppesen. 2011. Assessing lake typologies and indicator fish species for Italian natural lakes using past fish richness and assemblages. Hydrobiologia **671**:227–240.

Vondracek, B., and D. J. Degan. 1995. Among- and within-transect variability in estimates of shad abundance made with hydroacoustics. North American Journal of Fisheries Management **15**:933–939.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics **15**:393–425.

White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. Trends in Ecology and Evolution **22**:323–330.

Wilde, G. R., and K. L. Pope. 2004a. Relationship between lake-record weights of fishes and reservoir area and growing season. North American Journal of Fisheries Management **24**:1025–1030.

Wilde, G. R., and K. L. Pope. 2004b. Anglers' probabilities of catching record-size fish. North American Journal of Fisheries Management **24**:1046–1049.

Wilde, G. R., K. L. Pope, and B. W. Durham. 2003. Lure-size restrictions in recreational fisheries. Fisheries **28**:18–26.

Williams, G., K. L. Layman, and H. G. Stefan. 2004. Dependence of lake ice covers on climatic, geographic and bathymetric variables. Cold Regions Science and Technology **40**:145–164.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences **49**:2196–2218.

Winfield, I. J., M. Emmrich, J. Guillard, T. Mehner, and A. Rustadbakken. 2011. Guidelines for standardisation of hydroacoustic methods. WISER deliverable 3.4-3, European Commission.

Winfield, I. J., J. M. Fletcher, and J. B. James. 2007. Seasonal variability in the abundance of Arctic charr (*Salvelinus alpinus* (L.)) recorded using hydroacoustics in Windermere, UK and its implications for survey design. Ecology of Freshwater Fish **16**:64–69.

Winfield, I. J., J. M. Fletcher, J. B. James, and C. W. Bean. 2009. Assessment of fish populations in still waters using hydroacoustics and survey gill netting: Experiences with Arctic charr (*Salvelinus alpinus*) in the UK. Fisheries Research **96**:30–38.

Ylikarjula, J., M. Heino, and U. Dieckmann. 1999. Ecology and adaptation of stunted growth in fish. Evolutionary Ecology **13**:433–453.

Yule, D. L., J. D. Stockwell, D. R. Schreiner, L. M. Evrard, M. Balge, and T. R. Hrabik. 2009. Can pelagic forage fish and spawning cisco (*Coregonus artedi*) biomass in the western arm of Lake Superior be assessed with a single summer survey? Fisheries Research **96**:39–50.

Yvon-Durocher, G., J. Reiss, J. Blanchard, B. Ebenman, D. M. Perkins, D. C. Reuman, A. Thierry, G. Woodward, and O. L. Petchey. 2011. Across ecosystem comparisons of size structure: methods, approaches and prospects. Oikos **120**:550–563.

Zalewski, M., and R.J. Naiman. 1984. The regulation of riverine fish communities by a continuum of abiotic–biotic factors. Pages 3-9 in J.S., Alabaster editor. Habitat modification and freshwater fisheries. Batterworth Scientific Ltd, London, UK.

Declaration of authorship

I hereby declare that this PhD thesis has been written only by the undersigned and that no sources other than those indicated have been used. This thesis has not been submitted for a doctor's degree at any other institution. I am aware of the underlying doctorate regulation of the faculty this thesis is submitted to, Faculty of Agriculture and Horticulture of the Humboldt-University at Berlin.

Hiermit erkläre ich, die Dissertation selbständig und nur unter Verwendung der angegebenen Hilfen und Hilfsmittel angefertigt zu haben. Die Doktorarbeit wurde an keiner anderen Universität eingereicht. Ich erkläre die Kenntnisnahme der dem Verfahren zugrunde liegenden Promotionsordnung der Landwirtschaftlich-Gärtnerischen Fakultät der Humboldt-Universität zu Berlin.

Berlin, September 2012

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Matthias Emmrich

Appendix

Paper I

Heermann, L., **Emmrich**, **M.**, Heynen, M., Dorow, M., König, U., Borcherding, J., and Arlinghaus, R.

Explaining recreational angling catch rates of Eurasian perch, *Perca fluviatilis*: the role of natural and fishing-related environmental factors

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Explaining recreational angling catch rates of Eurasian perch, *Perca fluviatilis*: the role of natural and fishing-related environmental factors

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Abstract Angling catch records are frequently used to reveal fish population developments. It is therefore important to understand the determinants of angling catches. This study focused on angler-related, biotic and abiotic factors influencing catchability of Eurasian perch, *Perca fluviatilis* L. A multi-lake (21 lakes) study based on angling diaries collected in Mecklenburg-Vorpommern, Germany (2006/2007), found that angler-related factors such as fishing experience, species preference and bait/lure type had a large impact on perch catch rates. Additionally, environmental conditions (nutritional status and water transparency) affected either the size or the number of perch caught by anglers. Catch rates varied seasonally, which was confirmed by an experimental fishery on a gravel pit (2008). This portion of the study showed that altered food availabilities in the course of the year caused food limitation in perch, which in turn facilitated high catch rates and female-biased exploitation in autumn. It is concluded that both angler-related and abiotic factors interact affecting perch catch rates and size of perch captured in recreational angling.

KEYWORDS: catchability, diary, recreational fishing, sex-specific exploitation, starvation.

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Introduction

Recreational fishing is common throughout many freshwater ecosystems in temperate regions. It therefore represents a potentially valuable means to generate fishery-dependent data to infer insights about changes in fish populations (e.g. Lehtonen *et al.* 2009). Because a routine sampling protocol with scientific methods is often not possible in many recreational fisheries (Post *et al.* 2002; Daedlow *et al.* 2011), catch records from angler's diaries (e.g. collected by clubs) are often the only possibility to gather information on fish population developments (Cooke *et al.* 2000; Mosindy & Duffy 2007). This, however, demands that angler catch per unit effort (CPUE) is a reliable measure of fish population abundance, which is not necessarily the case (Erisman *et al.* 2011). Understanding how angling catch rates vary with abiotic and general limnological variables is important to interpret available angling records in the light of underlying population developments (Kuparinen *et al.* 2010).

Eurasian perch, *Perca fluviatilis* L. a widespread freshwater species in Europe, is a targeted angling species in many European countries such as Germany and Finland (e.g. Arlinghaus & Mehner 2004; Vainikka *et al.* 2012). Few studies on the catch aspects of Eurasian perch angling exist (Beardmore *et al.* 2011; Vainikka *et al.* 2012; but see e.g. Isermann *et al.* 2005; Irwin *et al.* 2008; Wilberg *et al.* 2008 for studies on yellow perch, *Perca flavescens* (Mitchill)), and there is no study that has investigated how environmental variables, such as lake morphometry, nutrient status and water transparency or season influence perch catch rates in perch recreational angling.

It is likely that catch rates of perch vary among lakes in relation to abundance of perch in line with prevailing ecological conditions. In general, high abundances of perch are found in relatively deep, vegetation-rich lakes with high water transparency and low to moderate nutrient concentrations (e.g. Persson *et al.* 1991; Jeppesen *et al.* 2000; Olin *et al.* 2002; Mehner *et al.* 2005). One would therefore expect catch rates of perch to peak under these environmental conditions. Vulnerability to angling is also related to individual behavioural traits (Uusi-Heikkilä *et al.* 2008) such as boldness (Mezzera & Largiadèr 2001). Perch activity correlates with nutritional status and hunger levels (e.g. Borcherding & Magnhagen 2008), predation risk (e.g. Bean & Winfield 1995) and temperature (Jacobsen *et al.* 2002). Thus, angling catchability of perch might not only depend on the lake's nutrient status, size and morphometry, but should also be influenced by other ecological factors, such as food availability or season.

In most recreational fisheries, positively size-selective exploitation is common (Lewin *et al.* 2006). This is the result of angler preference for large fish (Arlinghaus & Mehner 2003; Beardmore *et al.* 2011) and is further promoted by common management measures such as minimum length regulations (Arlinghaus *et al.* 2010). Moreover, morpho-physical aspects play an important role in the size selectivity as fish must be large enough to ingest a certain size of bait or lure. Moreover, individuals with higher growth potential and corresponding metabolic demands were shown to be more risk-prone and consume larger quantities of prey, and hence to be more vulnerable to capture in recreational fishing (Cooke *et al.* 2007; Redpath *et al.* 2010). In some freshwater top predators, such as pike, *Esox lucius* L., sex-specific differences in individual growth and associated behavioural differences were suggested to lead to a higher angling vulnerability of faster-growing female individuals resulting in sex-biased exploitation (Casselman 1975). Sex-specific growth differences also exist in Eurasian perch (Le Cren 1958) suggesting that perch vulnerability, but also the size of the perch angled, might be sex-dependent. The size of perch in the catch of anglers should also be connected to environmental variables because the size structure of perch populations strongly depends on competition and food availability connected to environmental limnological factors (e.g. Persson 1983, 1987; Claessen *et al.* 2000, 2002; Persson *et al.* 2004). A higher number of large-sized perch can be found in nutrient-poor lakes as the overall fish density and competition for food resources are low, such that individual perch can more easily reach the piscivorous stage (e.g. Jeppesen *et al.* 1997, 2000; Persson *et al.* 1998; Claessen *et al.* 2000) avoiding stunted growth (Ylikarjula *et al.* 1999).

In addition to natural factors, catchability of fish by anglers should also be correlated with a range of attributes of the angler, such as skill and fishing experience (e.g. McConnell *et al.* 1995; Arlinghaus & Mehner 2003), bait choice (Alós *et al.* 2009) or lure size (Wilde *et al.* 2003; Arlinghaus *et al.* 2008). While a clear effect of angler attributes on catchability and the size of fish captured has been reported in previous studies in different species (e.g. McConnell *et al.* 1995; Alós *et al.* 2009), limited information is currently available for perch (Beardmore *et al.* 2011).

The present study aimed at identifying factors influencing catch rates and size selectivity and sex selectivity of catches via angling for Eurasian perch focusing on: (1) angler-related factors (e.g. angling experience, angler's main target species or bait type); (2) environmental factors related to perch abundance and the size structure of perch populations (e.g. lake morphometry and nutritional status of the lake); and (3) factors related

to the ecology of perch (e.g. feeding or sex). In a first step, data from angling diaries collected over a 1-year period in 21 natural lakes of Mecklenburg-Vorpommern (hereafter, multi-lake study), Germany, were analysed with respect to modelling variance in perch catch rates and mean maximum length of perch harvested. This part of the study mainly focused on angler-specific and environmental influences. In a second step, a single-lake study was conducted in a gravel pit in North-Rhine Westphalia, Germany, to understand physiological/ecological constrains related to sex-specific feeding, which could not be addressed in the multi-lake study but was also expected to influence angling success and size of perch captured with angling gear.

Materials & methods

Assessing perch catches – multi-lake study

Data on perch catches by recreational anglers fishing in natural lakes in Mecklenburg-Vorpommern (M-V) were generated in a 1-year angling diary study described in detail by Dorow and Arlinghaus (2011). Briefly, over a period from September 2006 to August 2007, randomly recruited anglers fishing regularly in M-V were asked to record detailed information on a fishing-trip level including location, targeted species, angling method, overall and method-specific and species-specific effort, species-specific catch and harvest and the size of the largest fish harvested of a given species. In this study, only lake fishing trips where perch was the targeted species for at least some fraction of the trip, including zero-perch catch days, were incorporated. The data set was confined to lakes that were fished by at least three anglers throughout the entire study period. Furthermore, all lakes selected were fished at least during three of four seasons (spring: March, April, May), summer (June, July, August), autumn (September, October, November) or winter (December, January, February). Catch rate and mean maximum length of perch landed by 143 anglers targeting perch in 21 natural lakes were analysed. An individual angler average perch catch per unit effort (CPUE; fish h^{-1}) for each lake and season was estimated as the ratio of means (sum of perch catches divided by the sum of targeted perch fishing effort in hours), which is the best measure for completed angling trips (Pollock *et al.* 1994). As a second metric of interest, an index of perch length in the catch was calculated. No information on mean length of perch catches was available so the mean maximum length (L_{max}) of perch harvested was used as a size metric instead. L_{max} was enumerated as the mean of individual angler means of perch maximum length retained to reduce possible effects of outliers of rare catches of extreme-sized perch and to keep the angler the sampling unit. Note that L_{max} was only recorded in the diary in cases where perch were harvested and where individuals were ≥ 15 cm in total length (15 cm was a minimum size limit in some of the study lakes).

Assessing perch catches – single-lake study

Further data on perch catches orginiated from the single-lake study performed by means of experimental fishing in a single gravel pit lake, Lake Speldrop, situated in North-Rhine Westphalia, Germany (51°46′50″N, 6°22′42″E). The Secchi depth of the eutrophic lake in summer reaching chlorophyll-*a* concentrations of 20–50 $\mu g\ L^{-1}$ ranged between 1.1 and 8 m with a minimum at around the end of June. The lake has a surface area of about 7 ha, a mean depth of 7.4 m and is dominated by perch (for a more details, see Beeck *et al.* 2002; Borcher-ding *et al.* 2010). Gravel pit lakes differ structurally from natural lakes, by having steep banks, but quickly establish habitat features that are comparable to natural mesotrophic lakes. More than 20 000 gravel pits occur in Germany, of which over 1000 are situated in North-Rhine Westphalia (Berndt 1991). Therefore, such anthropogenically created ecosystems form water bodies typical for the landscape especially at the lower River Rhine (Berndt 1991). Former studies on perch populations in gravel pit lakes showed that the results are transferable to natural lakes (Beeck 2003).

Catch rates of perch were documented on one randomly chosen experimental angling sampling day per month from June to September 2008. On each sampling date, 4–6 experienced perch anglers distributed over 2–3 boats angled for 3–7 h using self-chosen sites. Anglers were spread over the whole lake but were angling mostly near the shore (15–20 m offshore). In each boat (staffed with 1–2 anglers), 3–4 fishing rods were used with either natural or artificial baits, where artificial baits were wobblers and spinners, and natural baits were mostly young-of-the-year (YOY) perch (about 60 mm) but sometimes also worms. In all but a few hours, both bait types were used simultaneously during the whole angling period, but anglers were free to choose the type of bait they used. Therefore, bait type was controlled, but size and type of natural or artificial bait were uncontrolled. As described earlier, catch rates of all perch caught with artificial and natural bait were expressed as CPUE (fish per rod-hour) including zero-catch values on a per boat basis. CPUE was calculated per boat and bait type; the resulting values were then averaged for each bait type and sampling day to compute the mean CPUE for each sampling date. Correspondingly, L_{max} of perch was calculated as the mean of the largest perch caught

in a given boat for natural and artificial bait on each sampling date. To analyse sex-dependent catch rates, the percentage of female perch caught was calculated.

Environmental correlates of perch catch rates in the multi-lake study

Nine predictors were selected to model variation in perch angling CPUE and L_{max} across lakes in M-V (multi-lake study). Five environmental variables known from literature to be related to perch abundance and size structure (Sumari 1971; Jeppesen *et al.* 2000), namely lake size (area, ha), depth (mean and maximum depth, m) and nutrient status [average annual total phosphorus concentration (TP, mg L^{-1}), average annual secci depth, cm], were selected (Table 1).

Measurements of TP and secci depth in all 21 study lakes were taken according to standardised protocols by local environment authorities between 2005 and 2008 with a minimum of three samplings per year and lake. Angling skill and timing of angling-related potential predictors of perch rates as estimated from the diary study and accompayning telephone and mail surveys with the same anglers were added as predictors (Dorow & Arlinghaus 2011). First, fishing trips were partitioned according to season (categorial into four seasons) and bait type (natural or artificial). Information on bait size was not available. Bait type and seasonality (co-varying with water temperature) are known to affect catch rate in various fish species (e.g. Margenau *et al.* 2003; Scrogin *et al.* 2004; Alós *et al.* 2009; Kuparinen *et al.* 2010). Moreover, since a range of angling skill and angler types were generating data, each angler contributing catch rate information was characterised by a measure of angling skill related to perch in terms of absolute angling experience (years of fishing) and preferred target species (e.g. non-predatory or predatory fish). The latter classification was required because Wilde and Ditton (1994) showed that the self-reported target species by anglers is predictably related to a degree of specialisation and commitment such that one can assume that a person who classifies himself or herself as a predatory fish, angler will likely be more skilled in catching predatory fish such as large perch. Target species was classified as 1 = no preference for a certain species; 2 = preference for non-predatory fish [e.g. roach, *Rutilus rutilus* (L.) bream, *Abramis brama* (L.) carp, *Cyprinus carpio* L.]; 3 = other (e.g. salmonids, marine species); and 4 = preference for predatory fish [e.g. perch, pike, zander, *Sander lucioperca* (L.)].

Table 1. Characteristics of the lakes investigated in the multi-lake study including area, mean depth (Z_{mean}), maximum depth (Z_{max}), secci depth (SD) and total phosphorus concentration (TP). In addition, number of anglers, number of fishing trips, proportion of the angler types fishing at each lake and their average fishing experience [FE (years) + standard deviation (SD)] from a sample of anglers taking part in a diary study are shown. Angler type: 1 = no preference; 2 = non-predatory fish; 3 = other (salmonids, marine species); 4 = predatory fish

								Angler type (%)				
Lake	Area (ha)	Z_{mean} (m)	Z_{max} (m)	SD (cm)	TP (mg L^{-1})	*N* Anglers	*N* trips	1	2	3	4	FE (SD)
Dobbertiner See	374.2	11.8	5.0	140	0.073	5	13	40.0	60.0	0.0	0.0	27.6 (11.3)
Fleesensee	1077.5	26.3	6.1	230	0.124	5	22	40.0	0.0	0.0	60.0	28.8 (16.8)
Glammsee	61.6	17.6	7.8	154	0.077	6	7	83.3	16.7	0.0	0.0	24.5 (23.3)
Groß Labenzer See	230.4	34.9	10.2	200	0.064	3	5	33.3	0.0	0.0	66.6	11.7 (7.6)
Großer Wariner See	260.1	9.5	4.7	90	0.129	5	13	80.0	20.0	0.0	0.0	25.2 (27.6)
Inselsee	1507.1	28.9	7.3	240	0.020	7	14	85.7	0.0	0.0	14.3	18.4 (11.6)
Keezer See	122.5	17.9	8.1	146	0.079	3	6	100.0	0.0	0.0	0.0	10.0 (6.6)
Kritzower See	66.1	12.7	5.9	246	0.059	7	15	85.7	0.0	0.0	14.3	32.4 (14.2)
Kummerower See	3254.8	23.3	8.1	155	0.051	12	31	75.0	0.0	8.3	16.7	37.3 (16.6)
Malchiner See	1395.2	10.0	2.5	37	0.081	4	21	75.0	0.0	0.0	25.0	31.3 (13.1)
Müritz	10331.0	31.0	28.1	300	0.018	33	347	51.5	12.1	9.1	27.3	31.5 (15.1)
Neumühler See	171.5	17.1	7.9	362	0.020	4	5	75.0	25.0	0.0	0.0	15.0 (14.1)
Orthsee	52.2	1.8	5.4	130	0.120	4	42	75.0	0.0	0.0	25.0	19.3 (8.7)
Plauer See	3840.0	25.5	6.8	258	0.030	8	15	62.5	37.5	0.0	0.0	25.5 (11.9)
Schweriner See	6153.8	52.4	11.5	701	0.048	28	125	71.4	7.1	3.7	17.8	21.1 (16.0)
Teterower See	336.3	10.7	4.0	64	0.123	5	32	40.0	0.0	0.0	60.0	17.8 (9.4)
Tollensesee	1789.6	31.3	17.7	435	0.041	6	58	100.0	0.0	0.0	0.0	27.8 (17.5)
Torgelower See	351.0	6.9	3.3	163	0.097	6	71	83.3	0.0	16.6	0.0	26.5 (18.3)
Zahrener See	70.3	7.9	3.2	47	0.071	3	8	33.3	66.7	0.0	0.0	31.0 (28.5)
Ziegelsee	299.8	34.4	8.9	358	0.041	8	24	75.0	0.0	0.0	25.0	19.1 (20.4)
Zierker See	347.3	3.5	1.6	58	0.116	4	4	50.0	50.0	0.0	0.0	25.8 (15.7)

Assessing nutritional status of perch in the single-lake study

In Lake Speldrop, not only size of captured perch was estimated, but all perch were killed in line with German animal protection legislation and examined for nutritional status and sex. Perch were measured (total length TL, mm), weighed (g), intestines removed and preserved in ethanol (96%) for stomach content analysis, and the sex of each individual recorded. As the number of perch caught with artificial bait was too low to analyse a possible change of perch diet across season (in total $n = 24$ individuals, but only three and four, respectively, in August and September), stomach content analyses were restricted to perch caught with natural bait. In the laboratory, stomach content analysis of 17–58 individuals per sampling date (in total $n = 167$) was carried out by weighing (to the nearest 0.01 mg) the full and empty stomach. Stomach contents were identified to genus level, and the food spectrum of each perch was expressed as the percentage composition of food items by weight (see Borcherding *et al.* 2007). The index of stomach fullness (ISF) for each fish (caught with natural bait) was calculated to describe the wet weight of the prey as a percentage of the perch's wet weight including stomach and stomach content (Hyslop 1980). Fulton's condition factor (Bagenal & Tesch 1978) was computed to obtain a measurement of the physiological condition of perch (caught with natural bait) as $K = 10^5 \times M / TL^3$, where M is the wet weight (g) and TL the total length (mm).

Statistical analyses – multi-lake study

Boosted regression tree (BRT) analysis (De'ath 2007; Elith *et al.* 2008) was used to explain the variance in perch angling catches in the multi-lake study using broad limnological and angling-skill-related indicators. BRTs can simultaneously handle categorical and continuous data. Predictor variables do not need to be transformed, outliers need not be eliminated, and predictors can strongly correlate (Breiman *et al.* 1984; De'ath 2007). A Poisson error distribution was selected for perch CPUE and a Gaussian error distribution for L_{max}. Predictive performance of the BRT models was evaluated using 10-fold cross-validation following the study by Elith *et al.* (2008). Model predictions were compared to withhold proportions of the data by dividing the total data set into ten mutually exclusive subsets that were randomly selected during cross-validation process. Model selection was based on the optimal number of trees producing the lowest prediction error without model overfitting by testing learning rates from 0.05 to 0.001, tree complexities (tc) of 1–5 and using bag-fractions of 0.5 and 0.75. The learning rate determines the contribution of each tree when added to the model, and lower learning rates are generally recommended. According to Elith *et al.* (2008), the minimum number of trees for the selection of the final model with the smallest residual deviance was set to 1000. Interactions between the predictor variables were modelled using tc with no interactions being included, if tc was one, one-way interactions included, if the tc was two and so on. The bag-fraction determined the proportion of the data, which are selected at each step (50% or 75% here). This introduced stochasticity to the model and improved accuracy and reduced over-fitting (Friedman 2002).

Boosted regression tree analysis does not generate P-values, but the relative influence of each predictor to total variance explanation can be used to assess the importance of each predictor. The measure of relative influence is based on the frequency a predictor is selected for splitting the tree and it is related to its influence on model improvement. Partial dependence plots were used to visualise the functional effects of individual predictors in the model on the response variable CPUE and L_{max} after accounting for the average effects of all other predictors (Friedman 2002).

In addition, bait type used and zero-perch catches were tested for seasonal variation using multiple sample tests for equality of proportions with continuity correction to account for small sample sizes (see e.g. Newcombe 1998). The function prop.test in the R programming language was used. In case of significant differences, Bonferroni-corrected pair-wise comparisons were made.

To test whether perch catch rates were influenced by seasonal preferences among different angler types, that is, whether a certain angler type preferred a certain season, a generalised linear model (GLM, binomial distribution) was used with perch CPUE as the response variable and angler type and season as factors. Analyses were conducted using the R statistical software system version 2.8.0 (R Development Core Team 2009) including the gbm package (Ridgeway 2006) and the custom code provided by Elith *et al.* (2008) for BRT analysis.

Assessing perch catches – single-lake study

Similar to the multi-lake study, the distribution of bait type used in the single-lake study was tested for seasonal differences using chi-squared tests. The effect of bait type and season on CPUE in Lake Speldrop was graphically assessed because of low sample sizes (n June/July/August = 3, September = 2). The same was true for the influence of season and bait type on L_{max}. One-way ANOVA and pairwise Bonferroni tests were used to

compare ISF of perch caught with natural bait across seasons. As Fulton's condition factor of perch caught is dependent on fish size (Froese 2006), ANCOVA with length as covariate and pairwise Bonferroni tests were used to test differences of condition of perch caught with natural bait across seasons. To understand whether the percentage of empty stomachs of perch caught with natural bait changed over the season, chi-squared tests were calculated. Chi-squared tests were also used to compare the percentage of females caught (with natural and artificial bait pooled) on each sampling date. Before calculating each ANOVA or ANCOVA, a Levene-test was computed to ensure homogeneity of variances ($P > 0.05$). Statistical analyses of Lake Speldrop data were conducted using SPSS, version 20 (SPSS IBM Corp., Armonk, New York, USA).

Results

Multi-lake study

In total, 8392 perch were reported caught during 878 fishing trips across the M-V lakes. Mean perch CPUE per angler ($n = 143$) averaged 2.4 [±2.5 standard deviation (SD)] fish h^{-1}. L_{max} of the largest perch harvested ($n = 119$ anglers) averaged 28.7 (±5.9 SD) cm with a maximum total length reported of an individual perch of 50 cm.

Final BRT models were run with learning rates of 0.005 (CPUE; $n = 2150$ trees) and 0.001 (L_{max}; $n = 2700$ trees). Interactions between the predictors were not included in the models (tc of 1) because they did not improve predictive performance substantially. Predictive performance was higher for the CPUE model (32.7%) compared with the L_{max} model (21.0%). The contribution of single predictors to variation in CPUE and L_{max} was highly variable and showed both linear and nonlinear patterns (Figs 1 & 2).

Highly influential variables on perch CPUE were angling-skill-related predictors (fishing experience, angler type) (Fig. 1). Furthermore, type of bait fished was important in affecting perch CPUE across the M-V lakes. In particular, fishing experience (years of fishing) had a large influence on angling success, with anglers having a long history of fishing (≥ 40 years) being the most successful. Furthermore, anglers who identified themeselves

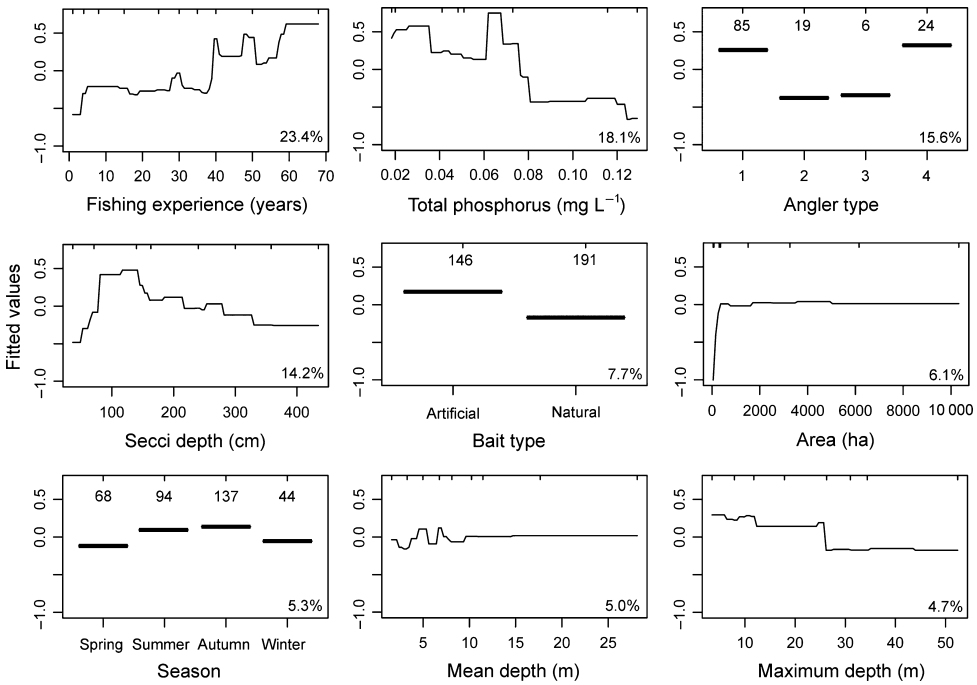

Figure 1. Partial effects of predictor variables on the angler catch per unit effort (CPUE, fish h^{-1}) of perch in lakes of Mecklenburg-Vorpommern (multi-lake study). Percentage values indicate the relative importance of the predictor variable in the boosted regression tree model. Rug plots on the top horizontal axes indicate the distribution of the predictor variables (*x*-axes), in deciles. In cases of categorical variables, sample size within each category is given on the top horizontal axes. Angler type: 1 = no preference; 2 = non-predatory fish; 3 = other (salmonids, marine species); 4 = predatory fish.

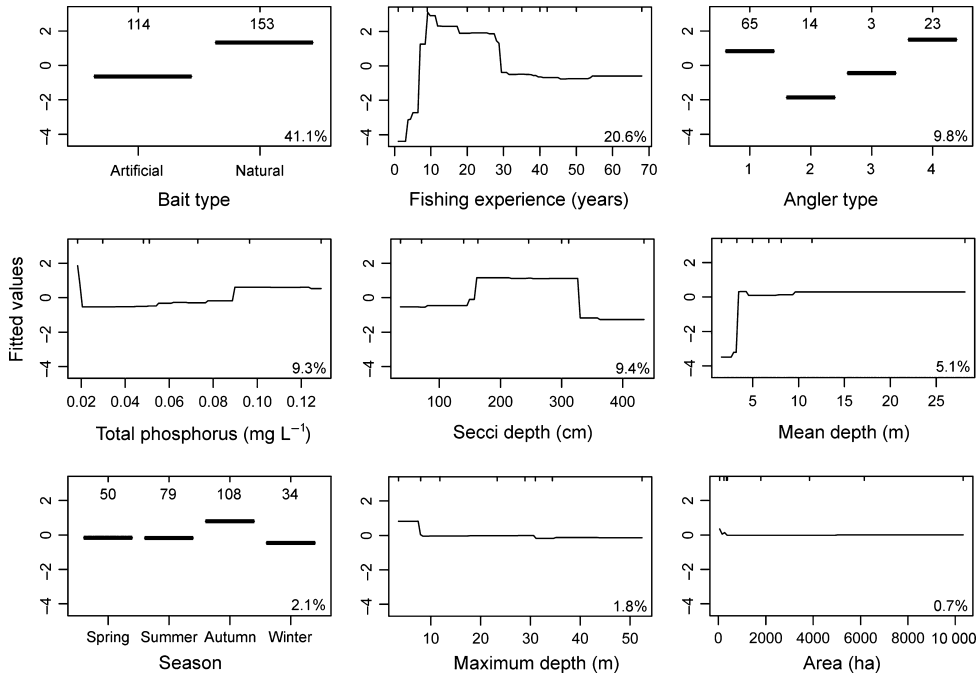

Figure 2. Partial effects of predictor variables on mean maximum length (L_{max}, cm) of perch caught by anglers in lakes of Mecklenburg-Vorpommern (multi-lake study). Percentage values indicate the relative importance of the predictor variable in the boosted regression tree model. Rug plots on the top horizontal axes indicate the distribution of the predictor variables (*x*-axes), in deciles. In cases of categorical variables, sample size within each category is given on the top horizontal axes. Angler type: 1 = no preference; 2 = non-predatory fish; 3 = other (salmonids, marine species); 4 = predatory fish.

as targeting predatory fish exhibited a higher perch CPUE, and in line with expectations, anglers identifying themselves as mainly targeting non-predatory fishes showed the lowest perch catch rates. However, anglers with no preference for a certain fish group had almost identical fishing success like anglers targeting predatory fish primarily. There was no seasonal preference of a certain angler type (GLM: interaction fishing type ~ season: $t = 0.35$, $P = 0.73$) indicating that the perch catch rates were not biased by different fishing intensities of the different angler types at certain seasons.

Anglers fishing with artificial lures caught more perch per hour of perch fishing than those engaged with natural bait (Fig. 1). In 56% of the fishing trips, anglers used natural baits with no significant seasonal change in the use of bait type ($\chi^2 = 1.5$, d.f. = 3, $P = 0.67$), suggesting that the results were not influenced by seasonal preferences of the anglers for a certain bait type.

Seasonal differences in perch CPUE were observed, with the highest perch catches observed during summer and autumn. However, the influcence of season on the total variation in perch CPUE was not strong. The proportion of zero catches differed significantly between the seasons ($\chi^2 = 10.5$, d.f. = 3, $P = 0.01$). A significantly higher ($P = 0.046$) proportion of trips with no perch caught was observed in spring (26.5%) than summer (15.2%). All other seasonal comparisons showed no significant differences ($P > 0.14$) in the proportion of zero-catch days (autumn: 17.1%; winter: 23.2%).

Predictors related to environmental conditions in lakes such as nutrient status (TP concentration) and water transparency also explained some of the variation in angler perch catches. Higher perch catch rates were obseved in oligotrophic and mesotrophic lakes (TP concentrations up to 75 μg L^{-1}) with water transparencies of 60–160 cm. Furthermore, perch CPUE was highest in lakes >400 ha, although the relative influence of lake area was weak (Fig. 2). Depth of the 21 lakes had no effect on the variation in angler's perch CPUE, but there were few shallow lakes with mean depth of <5 m in the data set (Table 1).

Bait type was the most influential predictor of size of perch landed in the BRT analysis (Fig. 2). Mean L_{max} of perch harvested by anglers using natural baits was higher than the anglers fishing with artificial lures. Furthermore, anglers with more than 8 years of fishing experience and

those targeting predatory fishes or showing no preference for a certain fish group caught on average larger perch than anglers with less fishing experience or those targeting non-predatory fishes, salmonids or marine fishes. The largest perch were caught in the most oligotrophic lakes and in lakes with Secchi depths ranging between 160 and 320 cm. Predictors related to lake morphometry (area, depth) and timing of angling had only weak influence on the size of perch caught by anglers.

Single-lake study

Thirty hours of angling over 5 days (one per month) by 14 anglers was carried out on Lake Speldrop; 191 perch were landed, 167 caught with natural bait and 24 with artificial bait. Natural baits were used slightly more frequently than artificial baits (artificial/natural = 2:3), but there was no significant seasonal change in the use of bait type (χ^2-test: $P > 0.05$), suggesting that the results were not influenced by seasonal preferences of the anglers for a certain bait type. Most perch caught by standardised angling ranged between 12 and 25 cm in size, which corresponded to the age-1 and age-2 cohorts. However, in June and August, a few trophy individuals around 45 cm long were landed. The mean CPUE (fish fishing rod^{-1} h^{-1}) varied strongly over the season peaking in September with a fivefold increase compared with other months (Fig. 3, no statistical tests possible). There was a tendency for CPUE obtained with natural baits exceeding the CPUE values generated with artificial baits (Fig. 3).

L_{max} of the largest perch harvested in Lake Speldrop averaged 22.1 (±44.1 SD) cm with a maximum total length of 48 cm. As with the Mecklenburg-Vorpommern data, there was no trend across season or bait type (data not shown).

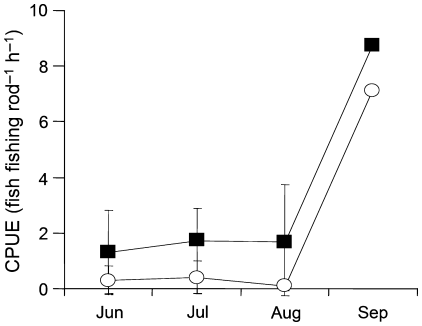

Figure 3. Angler catch per unit effort (CPUE, perch rod^{-1} h^{-1}) of perch caught with natural baits (black symbols) and artificial baits (white symbols) in Lake Speldrop (single-lake study) from June to September 2008. Error bars = standard deviation which was calculated if $n > 2$, n: June/July/August = 3, September = 2.

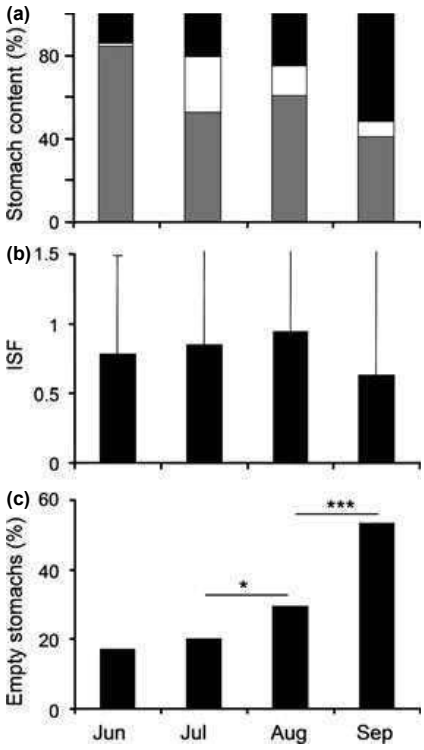

Figure 4. (a) Stomach content (%) of perch caught with natural baits in Lake Speldrop (single-lake study) from June to September 2008. Black bars = perch, white bars = macroinvertebrates, grey bars = zooplankton. (b) Index of stomach fullness (ISF) of perch caught with natural baits in Lake Speldrop (single-lake study) from June to September 2008. (c) Empty stomachs (%) of perch caught with natural baits in Lake Speldrop (single-lake study) from June to September 2008. Error bars = standard deviation, stars indicate level of significance of ANOVA (for ISF) or chi-squared tests (for empty stomachs): $***P \leq 0.001$, $*P \leq 0.05$. n for all panels: June = 47, July = 45, August = 17, September = 58.

Stomach content analysis of perch captured with natural baits zooplankton was the predominant food consumed in early summer (June), (Fig. 4a), consisting mainly of *Daphnia* spp. and *Chaoborus* larvae. During the summer, piscivory increased, and perch cannibalised on their own young-of-the-year (YOY), and in September, about 50% of all food items consumed were YOY perch. Macroinvertebrates played a marginal role in the diet of perch. While there were no significant changes of the ISF over the season (ISF about 0.7 for all months; ANOVA: $F_{3,163} = 0.63$, $P = 0.94$) (Fig. 4b), the percentage of empty stomachs significantly increased from July onwards (χ^2-test: June/July $P > 0.05$, July/August $P < 0.05$, August/September $P < 0.001$), and in September, 50% of fish landed had empty stomachs (Fig. 4c).

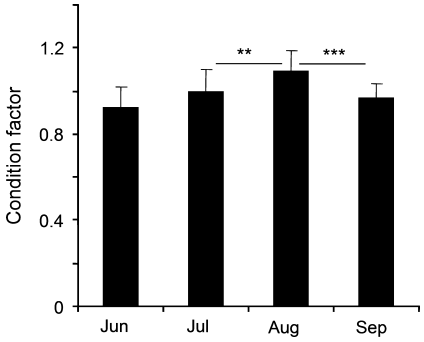

Figure 5. Condition factor of perch caught with natural baits in Lake Speldrop (single-lake study) from June to September 2008. Error bars = standard deviation, stars indicate level of significance of ANCOVA (length as covariate): $***P \leq 0.001$, $**P \leq 0.01$. *n*: June = 47, July = 45, August = 17, September = 58.

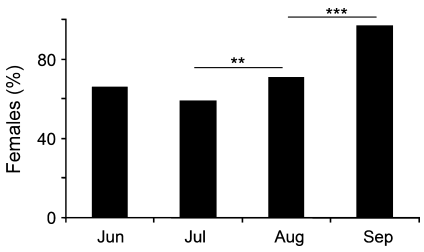

Figure 6. Proportion of females (%) of total catches of perch angled with natural baits in Lake Speldrop (single-lake study) from June to September 2008. Stars indicate level of significance of chi-squared tests: $***P \leq 0.001$, $**P \leq 0.01$. *n*: June = 47, July = 45, August = 17, September = 58.

The condition factor was the same in June and July (ANCOVA: $F_{3,235} = 34.4$, $P < 0.001$, Bonferroni tests: Jun/Jul $P = 0.32$) but increased from July to August (Fig. 5) (ANCOVA: $F_{3,235} = 34.4$, $P < 0.001$, Bonferroni tests: Jul/Aug $P < 0.01$). However, in September, the condition factor decreased (ANCOVA: $F_{3,235} = 34.4$, $P < 0.001$, Bonferroni tests: August/September $P < 0.001$).

In June and July, about 60% of perch caught were females (χ^2-test: June/July $P > 0.05$) (Fig. 6), increasing to 70% in August (χ^2-test: July/August $P = 0.01$) and almost all fish caught in September were females (97%, χ^2-test: August/September $P < 0.001$).

Discussion

Multi-lake study

This study found that perch catches by recreational angling are affected by angler-related factors, trophic lake characteristics and to lesser degree by lake morphometry and timing of angling. In the multi-lake study, angler-related attributes explained variance in catch rates, and to a lesser extent, size of perch harvested. Angling experience impacted both mean maximum length (L_{max}) of perch landed and catch rates of perch (CPUE). Both sharply increased after anglers passed a certain threshold of fishing experience (Figs 1 & 2). Only the very experienced anglers exhibited higher CPUE, while larger size of capture (L_{max}) occurred after only a few years of fishing experience. This, together with the lower predictive power of the length-based BRT model suggests that size of perch captured is less influenced by angler experience than CPUE, as found elsewhere (e.g. McConnell *et al.* 1995; Arlinghaus & Mehner 2003) and is interpreted as an increasing skill level positively affecting catch rates. It is, however, noteworthy that the peak size of perch captured occurred in younger age groups than the CPUE peak. This effect is possibly related to younger people using modern gear technology and fish finders to target trophy perch, while more experienced perch anglers seem to be better at achieving high catch rates because of their knowledge of the water body (cf. Eden & Bear 2011).

The self-rated target species preference (predatory or non-predatory fish) positively correlated with perch catch rates, with the highest CPUE achieved by anglers targeting predatory fish or anglers without any particular preference for a certain fish type. Both angler types are likely to be most committed (Wilde & Ditton 1994; Beardmore *et al.* 2011) and skilled in the capture of predatory fish such as perch, with the latter being more generic in their targeting behaviour, but also occasionally fishing for predators. By contrast, anglers identifying themselves as non-predatory fish anglers showed lower CPUE of the predatory fish perch. Similarly, the mean maximum length of perch harvested was highest for anglers targeting predatory fish or not targeting any specific species, which suggests greater skills in catching large perch.

Besides angler preferences for target species, bait type was another important variable affecting perch catch rates and size of fish caught, and similarly affected catch rates and size selectivity in other angling fisheries (e.g. Arlinghaus *et al.* 2008; Alós *et al.* 2009). Unfortunately, no data on bait size existed, so no effect of bait size on size of perch caught could be investigated. It is highly likely, however, that bait size will exert an effect on the size of perch captured (Wilde *et al.* 2003; Arlinghaus *et al.* 2008).

In angling in general, catching success is related to the motivation to ingest a bait, which can be connected to chemical components of the bait, its visual attractiveness and is moderated by bait size (reviewed in Løkkeborg & Bjordal 1992). Preferences of various fish

species for certain types of lures were shown to be season specific, size specific and species specific but also dependent on the experience an individual gained concerning certain bait types (reviewed in Løkkeborg & Bjordal 1992; Stoner 2004). Moreover, catchability with certain baits types (e.g. artificial baits) might be strongly dependent on angling pressure and previous exposure of the lures to individual fish (Beukema 1970; Kuparinen *et al.* 2010). In the present study, catch rates of perch by artificial baits were higher than those by natural baits in the multi-lake study. However, although artificial bait was more successive in catching a high number of perch, the largest individuals were hooked with natural baits across M-V, as described earlier for pike (Arlinghaus *et al.* 2008).

Fishing success was also found to be dependent on the environmental variables characterising the fished lakes. Perch populations are known to be related to the lake's morphometry, nutrient status, vegetation coverage and turbidity, abundance being highest in deep, vegetation-rich lakes characterised by low nutrient concentrations and high water transparency (Persson *et al.* 1991; Jeppesen *et al.* 2000; Olin *et al.* 2002; Mehner *et al.* 2005; Radke & Gaupisch 2005). In line with this, trophic status and water clarity exhibited a strong effect on perch catch rates in the present study. In particular, oligo-mesotrophic with intermediate Secchi depth produced the greatest perch CPUE rates, likely reflecting larger underlying population sizes. The weak effect of water depth and area on perch CPUE was probably caused by little contrast in the data, as most lakes in the multi-lake study were relatively deep and large (Table 1).

Total phosphorus concentration and Secchi depth were also the environmental factors that significantly affected mean maximum size of perch caught by anglers in the multi-lake study. The overall lower explanatory power of the size model indicated greater degree of stochasticity in catching large fish compared with catching large numbers of perch. This agrees with Wilde and Pope (2004) who documented a very low probability of catching record size fish in recreational fisheries. In other words, anglers have less control over size of fish captured than number of fish. In the present study, the largest fish were caught in the most nutrient-poor lakes with higher water transparencies. Nutrient-poor lakes are generally inhabited by greater numbers of large-sized fish than nutrient rich lakes where perch densities and competition between individuals and species are often higher reducing the individual's growth potential and the ability of perch to grow to a size where they can become cannibals (Jeppesen *et al.* 1997, 2000; Claessen *et al.* 2000; Emmrich *et al.* 2011).

Single-lake study

Studies on fish species other than perch found temperature-influenced and season-influenced angling catch rates (e.g. Margenau *et al.* 2003; Damalas *et al.* 2007; Kuparinen *et al.* 2010). Results of the multi-lake study also showed an increased CPUE in summer and autumn, and drastically increasing CPUE for perch in September in the single-lake study where catch rates varied across the seasons. Seasonal changes of body composition (Craig 1977), metabolic rate (Karas 1990), allocation of energy to gonads (Treasurer & Holliday 1981), behaviour (Uusi-Heikkilä *et al.* 2008) and, in particular, shoaling behaviour (Vainikka *et al.* 2012 and references therein) may be the important factors affecting the variability of catches throughout the season intimately linked to food availability and possible starvation and hunger. While rising temperatures will increase metabolic demand, catchability of perch is expected to peak if moderate to warm water coincides with suitable environmental conditions (e.g. oxygen) and lack of natural food, which according to the single-lake study, was present in late summer and autumn.

Stomach content analysis showed perch consumed *Daphnia* and *Chaoborus* larvae in early summer, but shifted to a cannibalistic diet in late summer. This diet shift possibly illustrates the normal ontogenetic development, as perch are known to shift to piscivory while growing (Thorpe 1977), but also may reflect a decrease in *Daphnia* and *Chaoborus* larvae (Beeck *et al.* 2002), causing alteration in diet. Svanbäck and Bolnick (2007) showed that by decreasing preferred prey abundances, perch are forced to switch to alternative prey sources suggesting that perch in Lake Speldrop shifted to piscivory because of decreasing zooplankton biomass. By using alternative resources, perch were able to maintain the amount being consumed, which is illustrated by the ISF as a measure for relative fullness of stomachs that did not change across season. Contrasting to ISF, the percentage of empty stomachs of larger perch caught increased throughout the season with increasing consumption of fish prey (to 50% in September). This is most likely attributable to two factors. First, although piscivorous individuals benefit from the energy-richer resource, potentially leading to higher growth rates (Galarowicz & Wahl 2005; Borcherding *et al.* 2010), attack and capture efficiency of prey fish are reduced compared with zooplankton (Galarowicz & Wahl 2005). Second, piscivorous perch vulnerable to natural baits used by anglers usually face a diminishing number of prey fish (YOY perch) over the season because of natural mortality but also because of higher predation pressure by larger perch (Beeck *et al.* 2002). Hence, it

appeared that satisfying the food demands became more difficult in late summer causing the shift to cannibalism. This food shortage existing in September in turn resulted in a drop in condition (see also Borcherding *et al.* 2007) likely elevating food demands, which in turn affected angling catch rates positively. Lack of food could then be the key explanation for higher catchability towards the end of summer in the present data.

Seasonal patterns in catch rates were accompanied by sex-biased exploitation patterns, which was most pronounced towards late summer. In June and July, about 60% of all perch landed were females. Although there are no data on the natural sex ratio for Lake Speldrop, previous studies showed that the ratio documented by angling in June and July in Lake Speldrop corresponded well to the natural sex ratio of other perch lakes (Jamet & Desmolles 1994; Rougeot *et al.* 2002). Surprisingly, perch caught in September were almost exclusively females (97%), suggesting that there were sex-specific reactions to food shortage in late summer (e.g. if females face greater energy intake they need to built up gonads) or the food shortage affected larger fish, which usually are females in perch, disproportionally. The sex-biased relative catchability might thus be explained by sex-dependent differences in growth (females grow up to 20% faster, Juell & Lekang 2001) and the elevated energy invested into gonads by females (Treasurer & Holliday 1981). This would result in higher energy demands by females, likely explaining the increased catch rates for female perch documented in the present study.

Conclusions

The results found that perch catch rates are strongly affected by angling-skill-related factors (fishing experience, angler type) and bait choice, but also reflected lake-specific limnological variables related to the trophic status of the lake (TP and Secchi depth). Because of the strong angler-type-related impacts on catch success the present results raise a cautionary note related to the use and interpretation of non-controlled angling diary data when used to infer population trends, as the reliability of the data will strongly depend on which angler type is reporting data. Another key finding related to seasonal patterns in perch catches is the female-biased exploitation coinciding with elevated hunger levels in late summer and autumn. Because (single-lake study) female perch were found to be particularly vulnerable to exploitation in periods other than winter time (see Vainikka *et al.* 2012 where no sex bias has been found in winter fishing for perch), autumn fishing activity in smaller water bodies could strongly bias sex-ratios and affect total fecundity, which in turn may affect recruitment, competition, predation control and subsequently population dynamics (Langangen *et al.* 2011). However, it has to be mentioned that further studies in multiple lakes should be conducted to clarify whether the patterns from the single-lake study are common across lakes.

Acknowledgements

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References

Alós J., Arlinghaus R., Palmer M., March D. & Alvarez I. (2009) The influence of type of natural bait on fish catches and hooking location in a mixed-species marine recreational fishery, with implications for management. *Fisheries Research* **97**, 270–277.

Arlinghaus R. & Mehner T. (2003) Socio-economic characterisation of specialised common carp (*Cyprinus carpio* L.) anglers in Germany, and implications for inland fisheries management and eutrophication control. *Fisheries Research* **61**, 19–33.

Arlinghaus R. & Mehner T. (2004) A management-orientated comparative analysis of urban and rural anglers living in a metropolis (Berlin, Germany). *Environmental Management* **33**, 331–344.

Arlinghaus R., Klefoth T., Kobler A. & Cooke S.J. (2008) Size selectivity, injury, handling time, and determinants of initial hooking mortality in recreational angling for northern pike: the influence of type and size of bait. *North American Journal of Fisheries Management* **28**, 123–134.

Arlinghaus R., Matsumara S. & Dieckmann U. (2010) Conservation and fishery benefits of saving old fecund pike

(*Esox lucius* L.) from recreational fishing with and without age-dependent maternal effects. *Biological Conservation* **146**, 1444–1459.

Bagenal T.B. & Tesch F.W. (1978) Age and growth. In: T.B. Bagenal (ed.) *Methods for Assessment of Fish Production in Fresh Waters*. Oxford: Blackwell Scientific Publications, pp. 101–136.

Bean C.W. & Winfield I.J. (1995) Habitat use and activity patterns of roach (*Rutilus rutilus* L.), rudd (*Scardinius erythrophthalmus* L.), perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) in laboratory: the role of predation threat and structural complexity. *Ecology of Freshwater Fish* **4**, 37–46.

Beardmore B., Haider W., Hunt L.M. & Arlinghaus R. (2011) The importance of trip context for determining primary angler motivations: are more specialized anglers more catch-oriented than previously believed? *North American Journal of Fisheries Management* **31**, 861–879.

Beeck P. (2003) *The Early Piscivory of European Perch (Perca fluviatilis)*: A Neglected Phenomenon with Notable Consequences for the Population Structure and Fish Community in Lake Ecosystems. PhD Thesis, Cologne: University of Cologne, 115 pp.

Beeck P., Tauber S., Kiel S. & Borcherding J. (2002) 0 + perch predation on 0 + bream: a case study on a eutrophic gravel pit lake. *Freshwater Biology* **47**, 2359–2369.

Berndt J.H. (1991) Ökologische Aspekte bei der Gestaltung und Nutzung von Baggerseen in der Aue. *Natur und Landschaft* **66**, 160–163.

Beukema J.J. (1970) Acquired hook-avoidance in pike *Esox lucius* L fished with artificial and natural baits. *Journal of Fish Biology* **2**, 155–160.

Borcherding J. & Magnhagen C. (2008) Food abundance affects both morphology and behaviour of juvenile perch. *Ecology of Freshwater Fish* **17**, 207–218.

Borcherding J., Hermasch B. & Murawski P. (2007) Field observations and laboratory experiments on growth and lipid content of young-of-the-year perch. *Ecology of Freshwater Fish* **16**, 198–209.

Borcherding J., Beeck P., DeAngelis D.L. & Scharf W.R. (2010) Match or mismatch: the influence of phenology on size-dependent life history and divergence in population structure. *Journal of Animal Ecology* **79**, 1101–1112.

Breiman L., Friedman J.H., Olshen R.A. & Stone C.J. (eds) (1984) *Classification and Regression Trees*. New York, NY: Chapman&Hall/CRC Press.

Casselman J.M. (1975) Sex-ratios of northern pike, *Esox lucius* Linnaeus. *Transactions of the American Fisheries Society* **104**, 60–63.

Claessen D., de Roos A.M. & Persson L. (2000) Dwarfs and giants: cannibalism and competition in size-structured populations. *American Naturalist* **155**, 219–237.

Claessen D., Van Oss C., De Roos A.M. & Persson L. (2002) The impact of size-dependent predation on population dynamics and individual life history. *Ecology* **83**, 1660–1675.

Cooke S.J., Dunlop W.I., MacLennan D. & Power G. (2000) Applications and characteristics of angler diary programmes in Ontario, Canada. *Fisheries Management and Ecology* **7**, 473–487.

Cooke S.J., Suski C.D., Ostrand K.G., Wahl D.H. & Philipp D. P. (2007) Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. *Physiological and Biochemical Zoology* **80**, 480–490.

Craig J.F. (1977) Body composition of adult perch, *Perca fluviatilis* in Windermere, with reference to seasonal changes and reproduction. *Journal of Animal Ecology* **46**, 617–632.

Daedlow K., BeardT.D. Jr & Arlinghaus R. (2011) A property rights-based view on management of inland recreational fisheries: contrasting common and public fishing rights regimes in Germany and the United States. *American Fisheries Society Symposium* **75**, 13–38.

Damalas D., Megalofonou P. & Apostolopoulou M. (2007) Environmental, spatial, temporal and operational effects on swordfish (*Xiphias gladius*) catch rates of eastern Mediterranean Sea longline fisheries. *Fisheries Research* **84**, 233–246.

De'ath G. (2007) Boosted trees for ecological modeling and prediction. *Ecology* **88**, 243–251.

Dorow M. & Arlinghaus R. (2011) A telephone-diary-mail approach to survey recreational fisheries on large geographic scales, with a note on annual landings estimates by anglers in northern Germany. *American Fisheries Society Symposium* **75**, 319–344.

Eden S. & Bear C. (2011) Reading the river through 'watercraft': environmental engagement through knowledge and practice in freshwater angling. *Cultural Geographies* **18**, 297–314.

Elith J., Leathwick J. & Hastie T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology* **77**, 802–813.

Emmrich M., Brucet S., Ritterbusch D. & Mehner T. (2011) Size spectra of lake fish assemblages: responses along gradients of general environmental factors and intensity of lake-use. *Freshwater Biology* **56**, 2316–2333.

Erisman B.E., Allen L.G., Claisse J.T., Pondella D.J., Miller E.F. & Murray J.H. (2011) The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 1705–1716.

Friedman J.H. (2002) Stochastic gradient boosting. *Computational Statistics & Data Analysis* **38**, 367–378.

Froese R. (2006) Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* **22**, 241–253.

Galarowicz T.L. & Wahl D.H. (2005) Foraging by a young-of-the-year piscivore: the role of predator size, prey type, and density. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 2330–2342.

Hyslop E.J. (1980) Stomach content analysis - a review of methods and their application. *Journal of Fish Biology* **17**, 411–429.

Irwin B.J., Wilberg M.J., Bence J.R. & Jones M.L. (2008) Evaluating alternative harvest policies for yellow perch in southern Lake Michigan. *Fisheries Research* **94**, 267–281.

Isermann D.A., Willis D.W., Lucchesi D.O. & Blackwell B.G. (2005) Seasonal harvest, exploitation, size selectivity, and catch preferences associated with winter yellow perch anglers on South Dakota lakes. *North American Journal of Fisheries Management* **25**, 827–840.

Jacobsen L., Berg S., Broberg M., Jepsen N. & Skov C. (2002) Activity and food choice of piscivorous perch (*Perca fluviatilis*) in a eutrophic shallow lake: a radio-telemetry study. *Freshwater Biology* **47**, 2370–2379.

Jamet J.L. & Desmolles F. (1994) Growth, reproduction and condition of roach (*Rutilus rutilus* (L)), perch (*Perca fluviatilis* (L)) and ruffe (*Gymnocephalus cernuus* (L)) in eutrophic Lake Aydat (France). *Internationale Revue der gesamten Hydrobiologie* **79**, 305–322.

Jeppesen E., Jensen J.P., Søndergaard M., Lauridsen T., Pedersen L.J. & Jensen L. (1997) Top-down control in freshwater lakes - the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* **342**, 151–164.

Jeppesen E., Jensen J.P., Søndergaard M., Lauridsen T. & Landkildehus F. (2000) Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwater Biology* **45**, 201–218.

Juell J.E. & Lekang O.I. (2001) The effect of feed supply rate on growth of juvenile perch (*Perca fluviatilis*). *Aquaculture Research* **32**, 459–464.

Karas P. (1990) Seasonal changes in growth and standard metabolic rate of juvenile perch, *Perca fluviatilis* L. *Journal of Fish Biology* **37**, 913–920.

Kuparinen A., Klefoth T. & Arlinghaus R. (2010) Abiotic and fishing-related correlates of angling catch rates in pike (*Esox lucius*). *Fisheries Research* **105**, 111–117.

Langangen O., Edeline E., Ohlberger J., Winfield I.J., Fletcher J. M., Ben James J. *et al.* (2011) Six decades of pike and perch population dynamics in Windermere. *Fisheries Research* **109**, 131–139.

Le Cren E.D. (1958) Observations on the growth of perch (*Perca fluviatilis* L.) over 22 years with special reference to the effects of temperature and changes in population density. *Journal of Animal Ecology* **27**, 287–334.

Lehtonen H., Leskinen E., Selen R. & Reinikainen M. (2009) Potential reasons for the changes in the abundance of pike, *Esox lucius*, in the western Gulf of Finland, 1939–2007. *Fisheries Management and Ecology* **16**, 484–491.

Lewin W.C., Arlinghaus R. & Mehner T. (2006) Documented and potential biological impacts of recreational fishing: Insights for management and conservation. *Reviews in Fisheries Science* **14**, 305–367.

Løkkeborg S. & Bjordal A. (1992) Species and size selectivity in longline fishing - a review. *Fisheries Research* **13**, 311–322.

Margenau T.L., Gilbert S.J. & Hatzenbeler G.R. (2003) Angler catch and harvest of northern pike in northern Wisconsin lakes. *North American Journal of Fisheries Management* **23**, 307–312.

McConnell K.E., Strand I.E. & Blake-Hedges L. (1995) Random utility models of recreational fishing: catching fish using a Poisson process. *Marine Resource Economics* **10**, 247–261.

Mehner T., Diekmann M., Brämick U. & Lemcke R. (2005) Composition of fish communities in German lakes as related to lake morphology, trophic state, shore structure and human-use intensity. *Freshwater Biology* **50**, 70–85.

Mezzera M. & Largiadèr C.R. (2001) Evidence for selective angling of introduced trout and their hybrids in a stocked brown trout population. *Journal of Fish Biology* **59**, 287–301.

Mosindy T.E. & Duffy M.J. (2007) The use of angler diary surveys to evaluate long-term changes in muskellunge populations on Lake of the Woods, Ontario. *Environmental Biology of Fishes* **79**, 71–83.

Newcombe R.G. (1998) Interval estimation for the difference between independent proportions: comparison of eleven methods. *Statistics in Medicine* **17**, 873–890.

Olin M., Rask M., Ruuhijarvi J., Kurkilahti M., Ala-Opas P. & Ylonen O. (2002) Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. *Journal of Fish Biology* **60**, 593–612.

Persson L. (1983) Effects of intra- and interspecific competition on dynamics and size structure of a perch *Perca fluviatilis* and a roach *Rutilus rutilus* population. *Oikos* **41**, 126–132.

Persson L. (1987) The effects of resource availability and distribution on size class interactions in perch, *Perca fluviatilis*. *Oikos* **48**, 148–160.

Persson L., Diehl S., Johansson L., Andersson G. & Hamrin S.F. (1991) Shifts in fish communities along the productivity gradient of temperate lakes-patterns and the importance of size-structured interactions. *Journal of Fish Biology* **38**, 281–293.

Persson L., Leonardsson K., Roos A.M.d., Gyllenberg M. & Christensen B. (1998) Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical Population Biology* **54**, 270–293.

Persson L., Claessen D., De Roos A.M., Byström P., Sjörgren S., Svanbäck R. *et al.* (2004) Cannibalism in a size-structured population: energy extraction and control. *Ecological Monographs* **74**, 135–157.

Pollock K.H., Jones C.M. & Brown T.L. (eds) (1994) *Angler Survey Methods and their Applications in Fisheries Management*. American Fisheries Society Special Publication 25). Bethesda, MD: American Fisheries Society.

Post J.R., Sullivan M., Cox S., Lester N.P., Walters C.J., Parkinson E.A. *et al.* (2002) Canada's recreational fisheries: the invisible collapse? *Fisheries* **27**, 6–17.

R Development Core Team (2009) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistcial Computing. (ISBN 3-900051-07-0).

Radke R. & Gaupisch A. (2005) Effects of phytoplankton-induced turbidity on predation success of piscivorous Eurasian perch

(*Perca fluviatilis*): possible implications for fish community structure in lakes. *Naturwissenschaften* **92**, 91–94.

Redpath T.D., Cooke S.J., Suski C.D., Arlinghaus R., Couture P., Wahl D.H. *et al.* (2010) The metabolic and biochemical basis of vulnerability to recreational angling after three generations of angling-induced selection in a teleost fish. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 1983–1992.

Ridgeway G. (2006) Gbm: generalized boosted regression models. R package version 1.6.3. Available at: http://cran.r-project.org/web/packages/gbm/index.html.

Rougeot C., Jacobs B., Kestemont P. & Melard C. (2002) Sex control and sex determinism study in Eurasian perch, *Perca fluviatilis*, by use of hormonally sex-reversed male breeders. *Aquaculture* **211**, 81–89.

Scrogin D., Boyle K., Parsons G. & Plantinga A.J. (2004) Effects of regulations on expected catch expected harvest, and site choice of recreational anglers. *American Journal of Agricultural Economics* **86**, 963–974.

Stoner A.W. (2004) Effects of environmental variables on fish feeding ecology: implications for the performance of baited fishing gear and stock assessment. *Journal of Fish Biology* **65**, 1445–1471.

Sumari O. (1971) Structure of perch population of some ponds in Finland. *Annales Zoologici Fennici* **8**, 406–421.

Svanbäck R. & Bolnick D.I. (2007) Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society of London, Series B* **274**, 839–844.

Thorpe J.E. (1977) Daily ration of adult perch, *Perca fluviatilis* L during summer in Loch-Leven, Scotland. *Journal of Fish Biology* **11**, 55–68.

Treasurer J.W. & Holliday F.G.T. (1981) Some aspects of the reproductive biology of perch *Perca fluviatilis* L. A histological description of the reproductive cycle. *Journal of Fish Biology* **18**, 359–376.

Uusi-Heikkilä S., Wolter C., Klefoth T. & Arlinghaus R. (2008) A behavioral perspective on fishing-induced evolution. *Trends in Ecology and Evolution* **23**, 419–421.

Vainikka A., Koskimäki J., Niemelä P.T. & Kortet R. (2012) Composition of the Eurasian perch (*Perca fluviatilis*) catches in ice fishing: does capture order predict body size? *Fisheries Research*, **115–116**, 24–30.

Wilberg M.J., Irwin B.J., Jones M.L. & Bence J.R. (2008) Effects of source-sink dynamics on harvest policy performance for yellow perch in southern Lake Michigan. *Fisheries Research* **94**, 282–289.

Wilde G.R. & Ditton R.B. (1994) A management-oriented approach to understanding diversity among largemouth bass anglers. *North American Journal of Fisheries Management* **14**, 34–40.

Wilde G.R. & Pope K.L. (2004) Relationship between lake-record weights of fishes and reservoir area and growing season. *North American Journal of Fisheries Management* **24**, 1025–1030.

Wilde G.R., Pope K.L. & Durham B.W. (2003) Lure-size restrictions in recreational fisheries. *Fisheries* **28**, 18–26.

Ylikarjula J., Heino M. & Dieckmann U. (1999) Ecology and adaptation of stunted growth in fish. *Evolutionary Ecology* **13**, 433–453.

Paper II

Emmrich, **M.**, Winfield, I.J., Guillard, J., Rustadbakken, A., Vergès, C., Volta, P., Jeppesen, E., Lauridsen, T.L., Brucet, S., Holmgren, K., Argillier, C., and Mehner, T.

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APPLIED ISSUE

Strong correspondence between gillnet catch per unit effort and hydroacoustically derived fish biomass in stratified lakes

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SUMMARY

1. Sampling of lake fish assemblages is a challenging task in fish science, and the information obtained strongly depends on the choice of sampling gear. The use of more than one sampling technique is generally preferred in order to achieve a comprehensive view on fish assemblage structure. Therefore, the knowledge of whether catches between fishing gears are comparable is crucial.
2. We compared catches in benthic multi-mesh gillnets with fish biomass estimates obtained by vertical hydroacoustics in 18 European lakes strongly varying in morphometry and trophic status. Separate analyses were conducted for different depth strata and for several fish length thresholds to account for depth- and size-selective gillnet catches.
3. Gillnet catches and hydroacoustically obtained fish biomass estimates were significantly correlated. The strength of correlations was independent of the fish length thresholds applied, but varied across different depth strata of the lakes, with the strongest correlations occurring in the shallow strata.
4. The results support the applicability of vertical hydroacoustics for the quantification of fish biomass in stratified lakes. Survey designs combining hydroacoustics with limited gillnetting at sampling dates shortly one after the other, the latter for the purpose of inventory sampling only, are a cost-effective strategy for sampling fish assemblages in lakes. However, gillnet sampling does not provide reliable fish density estimates in very deep lakes with separate, pelagic-dwelling fish assemblages.

Keywords: biomass estimates, fish sampling, gillnets, lakes, vertical hydroacoustics

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Introduction

Representative sampling of lake fish assemblages is a challenging task in fish science and management. The information obtained on the fish stock depends strongly on the choice of sampling method (Jackson & Harvey, 1997; Jurvelius, Kolari & Leskelä, 2011). Therefore, the use of more than one sampling technique is generally preferred in order to achieve a comprehensive overview of the abundance, species composition, size structure and spatiotemporal distribution patterns of fish (Kubečka *et al*., 2009). Furthermore, application of multiple gears may balance the fact that species caught as well as species size may vary with the gear type used (Bethke *et al*., 1999; Prchalová *et al*., 2009b).

The efficiency of passive types of sampling gear such as gillnets largely depends on the activity of the fish and estimates of fish abundance are accordingly indirect (Hamley, 1975). In contrast, fish sampled by active gear types such as trawls or hydroacoustics can be linked to the volume or area sampled, thus producing quantitative fish abundance estimates (Kubečka *et al*., 2012). However, local regulations or limited resources often set strict limits to the choice of sampling gears as well as the intensity of sampling. Thus, the knowledge of whether catches between fishing gears are comparable is crucial.

Fish assemblages in European lakes are nowadays primarily sampled by multi-mesh gillnets using standardised sampling designs [Appelberg *et al*., 1995; CEN (European Committee for Standardisation), 2005]. Catches by gillnets are used in both basic (Helland *et al*., 2007) and applied research, for example the assessment of ecological status of lakes from their fish assemblages required by the European Water Framework Directive (WFD; European Union, 2000; Søndergaard *et al*., 2005; Diekmann *et al*., 2005). However, representative gillnet sampling requires considerable effort with subsequent catch processing time and is therefore quite expensive (Dahm *et al*., 1992; Van Den Avyle *et al*., 1995). Furthermore, information on fish assemblage composition based on gillnet catches is relative and may not entirely correspond with absolute fish densities (Linløkken & Haugen, 2006; Prchalová *et al*., 2011) because of the species and size selectivity and the saturation effect of the nets depending on the number of fish entangled in the meshes (Olin *et al*., 2004; Prchalová *et al*., 2011). In most situations, gillnets are considered to be destructive as they kill most individuals entangled in the meshes if the nets are left for several hours in water at high temperatures or rapidly lifted from deep areas to the surface. As a result, the possibility that gillnets may have negative impact on fish population size cannot be excluded. In consequence, some European countries (e.g. U.K., Ireland, Belgium, Netherlands) often limit the intensive use of gillnet sampling because of low acceptance by the public and the recreational fisheries community (Winfield *et al*., 2009). This limitation hampers or even prevents scientific samplings of lake fish assemblages according to the European gillnet standard.

Recently, modern hydroacoustic equipment, a sophisticated active fishing technology which has evolved rapidly during recent times (Simmonds & MacLennan, 2005), has frequently been applied to sample fish assemblages particularly in large deep lakes. A combination of non-destructive fish sampling such as hydroacoustics combined with limited gillnetting is highly encouraged (Winfield *et al*., 2009; Harrison *et al*., 2010) and is likely to become more important in future (Kubečka *et al*., 2012). Currently, data from concurrent gillnet catches (e.g. species composition, relative species abundance) are used for the verification and interpretation of acoustic data because even state-of-the-art echosounders cannot yet distinguish between fish species. The combination of hydroacoustics and gillnets has frequently been applied in research on conservation of fish species (Winfield *et al*., 2009; Harrison *et al*., 2010), fish stock assessments (Mehner & Schulz, 2002; Deceliere-Vergès & Guillard, 2008) and fish behaviour (Helland *et al*., 2007).

However, previous comparisons of abundance data derived from gillnets and hydroacoustics in the same lake have shown very inconsistent and sometimes contrasting results. Peltonen *et al.* (1999) could not detect any significant correlation between gillnet catch per unit effort (CPUE) and areal fish abundance estimates obtained by hydroacoustics. Likewise, Dennerline, Jennings & Degan (2012) were unable to model a significant relationship between acoustically derived fish abundances and gillnet catches even after accounting for environmental covariables. Mehner & Schulz (2002) observed a significant correlation between gillnet and hydroacoustic fish abundances only if the smallest and largest fish were excluded from the analysis, and Elliott & Fletcher (2001) recorded a strong correlation only for large pelagic fish >20 cm. Even in a recently published multi-lake study on 14 Alpine lakes, no significant correlation between fish biomass estimates derived from hydroacoustics and gillnets could be detected (Achleitner, Gassner & Luger, 2012). Obviously, the correspondence between gillnet catches and hydroacoustically obtained fish abundances is weak and/or complex owing to differences in size selectivity of the gears or differences in sampling intensity and date of sampling in different lake habitats.

In this study, we sampled fish assemblages in 18 natural European lakes located in different ecoregions using standardised benthic multi-mesh gillnetting (CEN, 2005) and vertical downward-looking hydroacoustics. Ours is, to our knowledge, the largest data set published comparing fish abundance estimates obtained from these two types of sampling gears. The aim of our study was to test the correspondence between fish biomass caught per unit effort (BPUE) from gillnets and area-related fish biomass derived from hydroacoustics. Separate analyses were conducted for different depth strata and for several fish length thresholds to account for depth- and size-selective gillnet catches. We hypothesised that correspondence between gears improves using standardised sampling techniques and considering the entire lake as a single sample unit by pooling catches from all gillnets and reflected energy from fish from all hydroacoustic transects in contrast to the above cited tests where single gillnets or hydroacoustic transects within lakes were treated as sample units.

Methods

Study lakes

We analysed fish sampling data from 18 natural lakes located in seven European countries. The study sites covered a latitudinal range of 15° and were located in lowland up to mountain regions (Fig. 1 and Table 1). The lakes differed substantially in surface area (0.25–5.45 km^2) and had very different shapes representing circular, elongated and branched lake surface types. All lakes except Lake Fussing (Denmark) were thermally stratified during summer. The mean depth of most lakes varied between 3.8 and 13.6 m and maximum depth between 7.8 and 35.0 m. However, three very deep lakes with mean depth >30 m and maximum depth >70 m were sampled additionally (Table 1). The trophic status of the lakes based on the total phosphorus concentration ranged from oligotrophic to hypertrophic (Table 1).

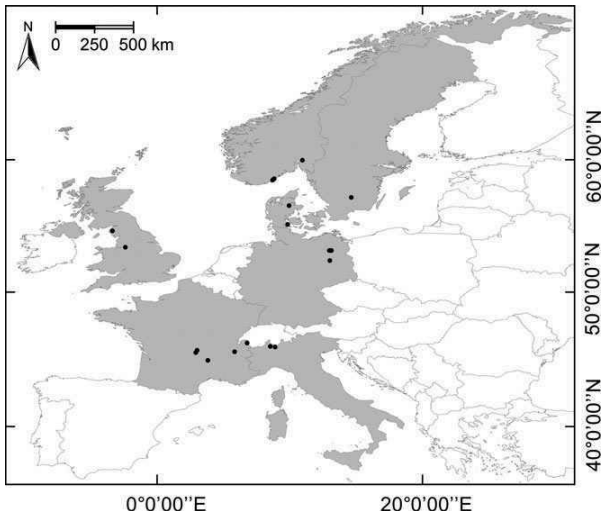

Fig. 1 Geographical location (closed circles) of the 18 lakes distributed across seven European countries (grey-coloured) whose fish assemblages were sampled by vertical hydroacoustics and standardised benthic multi-mesh gillnets.

Gillnet sampling

Fish assemblages were sampled consistently across all countries following a stratified random design accredited as the European standard (EN 14757) for sampling fish with multi-mesh gillnets in lakes (CEN, 2005). Sampling took place between 2005 and 2010. In all lakes, the same type of benthic multi-mesh gillnets (type NORDIC) was used. The nets, made of non-coloured, monofilament nylon, were each 30 m long and 1.5 m high (=45 m^2) and consisted of 12 panels of 2.5 m each with mesh sizes ranging from 5 to 55 mm knot to knot (bar mesh size). The mesh sizes followed a geometric series (43, 19.5, 6.25, 10, 55, 8, 12.5, 24, 15.5, 5, 35, 29 mm) with an almost constant ratio between two adjacent different mesh sizes of *c.* 1.25. Depending on lake area and maximum depth, predetermined numbers of nets were set randomly within different lake depths. The different depth zones of a lake were divided into a maximum of eight layers, and these are termed depth strata (CEN, 2005): lake surface to 2.99 m depth, 3–5.99 m, 6–11.99 m, 12–19.99 m, 20–34.99 m, 35–49.99 m, 50–74.99 m, ≥75 m (all depths measured relative to surface). Fish assemblages were sampled between summer and autumn (end of July–mid-October, Table 1) to maximise catch efficiency of the gillnets before the usual reduction of lake temperatures in the epilimnion to <15 °C. In accordance with the standard, the gillnets were set overnight to ensure that the activity peaks of the fish during dusk and dawn were included (Prchalová *et al.*, 2009b). Weighting of the gillnet catches after retrieval was not necessary, because all nets were soaked for *c.* 12 h.

The captured fish were determined to species level, measured to the nearest mm total length (TL) and weighed to the nearest g fresh mass (FM). For the Danish lakes, individuals were pooled according to species and counted, and total FM was measured. For the Swedish lake, individual fish lengths were available with pooled FM. Biomass per unit effort (BPUE) was calculated as the average biomass of fish (kg FM) caught by one net during one night. Additionally, depth strata–specific BPUE values were calculated by summing up the FM of all fish caught

Table 1 Characteristics of the study lakes including latitudinal (Lat) and longitudinal (Long) coordinates (WGS84), altitude [Alt (m a.s.l.)], area (km^2), mean depth [Z_{mean} (m)], maximum depth [Z_{max} (m)] and total phosphorus concentration [TP ($\mu g\ L^{-1}$)]. In addition, sound frequencies of the hydroacoustic systems [Freq (kHz)], number of hydroacoustic transects (n Tr), degree of coverage (DoC), number of benthic gillnets (n GN) and sampling month of gillnetting are given

Country	Lake	Lat	Long	Alt	Area	Z_{mean}	Z_{max}	TP	Freq	n Tr	DoC	n GN	Month
Denmark	Fussing	56.4705	9.8722	18	2.17	12.6	28.1	40	200	11	3.8	17	August
	Nordborg	55.0575	9.7638	6	0.54	5.0	7.8	241	200	12	3.1	13	September
France	Aiguebelette	45.5555	5.7985	374	5.45	30.7	71.0	10	70	12	5.3	58	October
	Aydat	45.6641	2.9861	837	0.56	8.0	15.0	20	70	11	6.9	24	September
	Bouchet	44.9091	3.7906	1200	0.43	15.0	28.0	27	70	6	5.7	24	September
	Montriond	46.2090	6.7283	1060	0.33	9.0	19.7	14	70	9	3.7	16	September
	Pavin	45.4956	2.8875	1196	0.45	45.0	96.0	20	70	9	6.9	32	September
Germany	Glindow	52.3568	12.9284	33	1.95	4.9	14.3	139	120	18	4.7	24	September
	Grienerick	53.1067	12.8873	56	0.87	4.3	14.1	37	120	8	4.0	24	September
	Roofen	53.1087	13.0397	59	0.57	9.0	19.1	17	120	18	5.6	24	September
Italy	Ghirla	45.9166	8.8222	415	0.25	11.0	14.0	24	120	17	7.3	16	October
	Mergozzo	45.9561	8.4643	204	1.82	45.6	73.0	6	120	12	7.0	32	October
Norway	Longumvatnet	58.4880	8.7529	32	1.00	9.6	35.0	10	70	19	3.9	32	August
	Nøklevann	59.8751	10.8748	163	0.79	11.3	33.0	5	70	17	4.1	32	August
	Temse	58.3835	8.6370	15	0.62	5.0	10.0	16	70	6	3.4	24	September
Sweden	Fiolen	57.0827	14.5331	226	1.56	3.8	10.0	13	70	9	4.5	24	July
U.K.	Loweswater	54.5830	−3.3562	125	0.60	8.4	16.0	13	200	12	5.6	17	August
	Rostherne Mere	53.3542	−2.3858	27	0.48	13.6	31.0	180	200	13	7.2	22	August

within a given stratum and dividing it by the number of nets set in that stratum. The gillnet catches were also used to calculate an overall length–mass relationship (LMR) by including all fish from all lakes, independently of their taxonomy, for which information of individual length and individual mass was available. We refrained from developing lake-specific LMR to limit the potential sources of variability in the analyses. Catches from pelagic gillnets, deployed as only a single vertical row at the deepest part of the lakes, were not considered in this study because they were inconsistently used among the countries.

Hydroacoustics

Data collection. Hydroacoustic fish monitoring did not follow an established standard protocol because such a protocol does not yet exist for European waters (Kubečka *et al.*, 2009; Winfield *et al.*, 2011). However, earlier studies have demonstrated that hydroacoustic equipment from different manufacturers operated by different expert teams produces comparable fish density estimates (Mehner *et al.*, 2003; Wanzenböck *et al.*, 2003). Most lakes were sampled by hydroacoustics on dates within the time period of the corresponding gillnet surveys. Only in Lakes Fussing and Fiolen was hydroacoustics performed two and eight weeks after the gillnetting, respectively. Four expert teams collected the data, all using vertical downward-looking split-beam echosounders. The Danish and U.K. lakes were insonified with a Biosonics-DT-X echosounder (Biosonics Inc., Seattle, WA, U.S.A.) equipped with a DT-200-0615-033 transducer. In all other lakes, Simrad EK60 systems (Simrad Kongsberg Maritime AS, Horten, Norway) equipped with one of three types of transducers (ES120-7C, ES70-11 and ES70-11C) were used. The echosounders operated at frequencies of 200 kHz (Biosonics), 120 and 70 kHz (Simrad) (Table 1) using pulse durations between 256 μs and 512 μs and sample intervals of 2–5 pulses s^{-1} depending on local lake conditions. Transmission power ranged between 80 and 500 watt. Calibration of the systems was undertaken on a regular basis according to the operator manuals using standardised targets.

Acoustic measurements on fish populations can be affected by the sound frequency and pulse duration (Knudsen, Larsson & Jakobsen, 2006; Godlewska *et al.*, 2011), but it has been shown that parameters lying within the range of this study produce unbiased fish biomass estimates (Guillard, Lebourges-Dhaussy & Brehmer, 2004; Godlewska *et al.*, 2009, 2011). Nevertheless, we analysed the effects of the different sound frequencies and pulse durations on the reliability of the fish density estimates using the Sawada index N_v (Sawada, Furusawa & Williamson, 1993) (see Statistics).

For the majority of the lakes, the survey designs consisted of non-overlapping, parallel transects. In case where a zig-zag design was used or if transects crossed each other, a representative subset of transects covering all parts of the lake was selected for post-processing. This

allowed us to generate an approximately parallel survey design for all lakes. The hydroacoustic sampling effort was determined *a priori* following the approach of Aglen (1983) by calculating the degree of coverage, defined as the ratio between the surveyed distance, that is, the cumulative length of the hydroacoustic transects (km), and the square root of the lake area (km^2). As a general guide, the degree of coverage should be at least 3.0 and preferably near to or above 6.0.

We decided to use only night-time hydroacoustic data as fish are usually better detected by hydroacoustics during darkness when individuals are more dispersed in the open water (Appenzeller & Leggett, 1992; Mehner, Kasprzak & Hölker, 2007b). This pattern was also confirmed in five of the study lakes where both daytime and night-time data were analysed (M. Emmrich, unpublished). Echoes were recorded at an average boat speed of 1.88 m s^{-1} (SD: 0.44), which equals 6.77 km h^{-1} [range: 2.6–8.6 km h^{-1} (mean per lake)], and stored in a digital format on laptop computers.

Data post-processing. All raw files were converted with a base threshold of −100 dB and a minimum single target size of −80 dB into a format compatible to be processed with the Sonar5-Pro software (version 6.01; Balk & Lindem, 2011). The analysis of the hydroacoustic data was kept as standardised as possible and was carried out by the same individual researcher. For each transect, the bottom line was automatically detected by the Sonar5-Pro software using pre-defined settings based on the authors' experience and subsequently manually corrected if necessary. All files were additionally checked for the presence of unwanted non-fish echoes (e.g. air bubbles, submerged macrophytes, debris accumulation, ropes from gillnets/buoys, fake bottom echoes) that were manually deleted from the echograms.

Sonar5-Pro software was also used to calculate total mean volumetric backscattering strength [S_v in decibels (dB)] from the fish echoes. To estimate fish biomass, echo integration (sv/ts scaling) was used. All chosen hydroacoustic transects of a lake were merged into a single file and analysed together. We did not divide the transects into horizontal segments elementary distance sampling units (EDSU) to avoid high numbers of empty cells with no backscattered echo energy. Furthermore, the small variability of our sampling designs can create geostatistical variance patterns owing to spatial autocorrelation, a problem that is avoided if S_v is calculated for the entire insonified water volume.

Calculations of S_v and areal fish biomass excluded water layers from surface down to 2 m because for the Danish and U.K. lakes, shallower parts were not recorded during field campaigns. This exclusion functioned further as a trade-off to reduce the effects of possible avoidance reactions of fish from the vessel, to consider the transducer depth and to account for the upper blind zone (near-field of the transducer) that gives unreliable fish echoes, but still insonifying some volume of surface water. For the comparison of fish biomass in the upper depth stratum defined by the gillnet standard (0–2.99 m; CEN, 2005), we applied the fish biomass detected in 2–3 m depth to the upper metres (0–1 m and 1–2 m). Echoes from fish close to the lake bottom cannot always be distinguished from the bottom echo such that the bottom margin was set to 0.3 m (lower blind zone).

In addition to the analysis covering the entire water volume, depth strata of the merged hydroacoustic files were analysed separately to identify for which depths benthic gillnet catches corresponded with hydroacoustic estimates. It has been recommended to estimate fish biomass from *in situ* target strength data in defined depth strata with homogeneous fish species and size structure (Parker-Stetter *et al.*, 2009). However, for a direct, depth-specific comparison, we used the same depth strata that have been *a priori* defined according to the gillnet standard (CEN, 2005). Homogeneous size distributions of single echo detections (SED) could be confirmed for the upper depth strata in most lakes. However, with increasing thickness of the depth strata applied only in the deeper lakes, slightly more non-homogeneous patterns in SED size distributions were observed (M. Emmrich, unpublished).

The hydroacoustic data were also checked for reliable estimates of *in situ* target strength using the Sawada index N_v (number of fish per acoustic sampling volume) (Sawada *et al.*, 1993). The index serves as a diagnostic tool for the identification of volumes with very high fish densities. If $N_v > 0.1$, data were interpreted with appropriate caution.

For the conversion of the echo target strength (TS in decibel, dB) into fish total length (TL in cm), the relationship of Love (1971) was used, adjusted to the different sound frequencies (f) of 70, 120 and 200 kHz.

$$TS = 19.1 \times \log(TL) - 0.9 \times \log(f) - 62$$

By applying this general conversion formula, we avoided introducing additional uncertainty into the comparison of biomass between both fishing gears. For the conversion of the hydroacoustic fish lengths into fish biomass, we used the LMR calculated from the pooled gillnet catches from all lakes (see Gillnet sampling), because

gillnet catches from all lakes (except Montriond) were dominated by the same species (Table 1).

We further tested whether certain fish size thresholds affected the correspondence between the two sampling gears. Previous studies have shown that small fish are not effectively caught with multi-mesh gillnets (Olin, Malinen & Ruuhijärvi, 2009; Prchalová *et al.*, 2009b) because of the small ratio between diameter and mesh size for the smallest meshes, which reduces the stretchability of the meshes and the catchability of small fish (Hamley, 1975), and the saturation effect of the gillnets at high densities of small fish. Therefore, stronger correspondence between gillnet catches and hydroacoustically derived fish abundance might be achieved if small fish are excluded from the comparison (Mehner & Schulz, 2002).

To evaluate the effect of variable lower fish sizes on the analysis, we selected TS thresholds (SED/Amp mode) of −58/−64 dB, −52/−58 dB and −47/−53 dB which equal fish TL of *c.* 2, 4 and 8 cm according to the TS–TL relationship of Love (1971). For these small fish, the correspondence between fish TL and TS was similar for all three sound frequencies. As also very large fish are not effectively caught with multi-mesh gillnets having a maximum mesh size of 55 mm knot to knot (Psuty & Borowski, 1997), we also tested a maximum size threshold of 60 cm equivalent to TS values >−30 dB. The 60-cm threshold was the upper size range representing 99.9% of all fish caught by the nets.

To account for a potential modification of LMR by the exclusion of small fish, an additional LMR for fish ≥8 cm was calculated and integrated into the Sonar5-Pro software for the conversion of the hydroacoustically detected fish echoes into fish biomass. The effect of applying a minimum fish length threshold of 2 and 4 cm or a maximum fish length threshold of 60 cm on LMR was marginal owing to the small number of fish with minimum and maximum size in the gillnet catches.

Statistics

Biomass caught per unit effort values and hydroacoustically derived areal fish biomasses were $\log_{10}$ (x + 1)-transformed to meet assumptions of bivariate normality and homogeneity of variances. S_v values (in dB) did not need to be transformed as they are already on a log-scale and fulfilled the assumptions for parametric test statistics. Pearson's product–moment correlations were calculated to test for the linear relatedness of gillnet BPUE with either hydroacoustic S_v or areal fish biomass (kg ha^{-1}).

To predict areal fish biomass from given BPUE values, ordinary least-squares (OLS) regression was used with gillnet BPUE as the independent variable and hydroacoustically derived areal fish biomass as the dependent variable. We chose OLS regression instead of model II regression (e.g. major axis regression), because we aimed to predict areal fish biomasses from gillnet catches (BPUE). In this case, OLS regression can be used in model II situations, because it produces fitted values with the smallest error (Legendre & Legendre, 1998). However, as the independent variable (BPUE) was also measured with an unknown error term, we did not calculate reliability estimates (95% confidence intervals). Furthermore, the regression lines presented cannot be used to predict gillnet catches (BPUE) from quantitative fish biomass estimates derived from hydroacoustics. Intercepts of the regression lines were tested for a significant deviation from zero to determine whether zero catches in gillnets also resulted in the prediction of zero fish biomass from hydroacoustics.

To test the effects of the different sound frequencies and pulse durations on the reliability of fish density estimates (expressed by the Sawada index N_v), we used a generalised linear model (GLM) with N_v as the response variable and sound frequency and pulse duration as factors. Calculations were made using the R statistical software package version 2.10.0 (R Development Core Team, 2009).

Results

Benthic gillnet catches

In total, 455 nets caught 21 067 fish representing 35 species from 15 families. Mean number of fish caught in the lakes was 1170 individuals (SD: 1093; range: 152–3534). The number of species per lake caught by gillnets ranged between three and 14. Perch (*Perca fluviatilis* L.) and roach [*Rutilus rutilus* (L.)] dominated the catch in most lakes (Table 2) and also dominated the overall gillnet catch (perch: 59.6% of number and 39.3% of biomass; roach: 24.5% of number and 30.7% of biomass). Mean size of fish caught was 11.3 cm (SD: 6.4) and 38.5 g (SD: 150.3) with a maximum individual TL of 88.0 cm and a FM of 6229 g. Minimum TL of fish caught was 2.0 cm. However, very small (2–4 cm) and very large (>60 cm) fish were rarely caught (n = 8 and n = 15, respectively). The overall numerical proportion of fish <8 cm TL in the gillnet catches was 37.9%, but differed between the lakes (0–74.9%).

Biomass caught per unit effort values of single nets ranged between 0 and 11.15 kg net^{-1} night^{-1} (mean 1.79 kg; SD:

Table 2 Species richness (SR) and the two dominant species (numerical abundance) in the benthic gillnet catches

Lake	SR	Abundance (%)
Fussing	6	PEF (84.0) RUR (13.3)
Nordborg	9	RUR (43.0) GYC (18.1)
Aiguebelette	12	RUR (48.3) PEF (38.4)
Aydat	7	RUR (52.0) PEF (31.0)
Bouchet	11	RUR (68.4) PEF (9.2)
Montriond	7	PHP (59.7) LES (21.6)
Pavin	6	PEF (75.5) SAU (10.8)
Glindow	9	PEF (45.3) RUR (24.3)
Grienerick	11	PEF (52.5) RUR (32.9)
Roofen	11	PEF (71.7) RUR (23.0)
Ghirla	6	PEF (57.0) RUR (28.4)
Mergozzo	14	RUR (60.4) GYC (15.0)
Longumvatnet	4	PEF (55.8) SCE (43.0)
Nøklevann	6	PEF (73.0) RUR (22.2)
Temse	5	PEF (94.7) CO sp. (3.8)
Fiolen	4	PEF (62.6) RUR (25.2)
Loweswater	4	PEF (99.1) ESL (0.4)
Rostherne Mere	3	PEF (84.6) RUR (15.3)

Species codes (scientific names): CO sp. (*Coregonus* sp.), ESL (*Esox lucius* L.), GYC (*Gymnocephalus cernuus* L.), LES (*Leuciscus souffia* RISSO), PEF (*Perca fluviatilis* L.), PHP [*Phoxinus phoxinus* (L.)], RUR [*Rutilus rutilus* (L.)], SAU (*Salvelinus umbla* L.), SCE [*Scardinius erythrophthalmus* (L.)]

2.16). The proportion of empty nets in a lake ranged between 0 and 37.5%. In 14 of 18 lakes, the maximum depth-specific average BPUE values were observed in the two shallowest strata (0–5.99 m).

The length–mass relationship (LMR) for all fish captured in the 18 lakes was

$$FM\ (g) = 0.00956\ TL\ (cm)^{3.033}\ (r^2 = 0.96;\ P < 0.001;\ n = 15\ 804).$$

After removing fish <8 cm from the data set, the LMR changed into

$$FM = 0.00762\ TL^{3.116}\ (r^2 = 0.97;\ P < 0.001;\ n = 10\ 199).$$

Hydroacoustics

Mean total S_v averaged −62.8 dB (SD: 10.5) by applying a minimum length threshold of ≥2 cm TL, −61.1 dB (SD 8.3) for the fish TL threshold ≥4 cm and −62.1 dB (SD: 8.4) for the fish TL threshold ≥8 cm. Hydroacoustically derived areal fish biomass averaged 88.4 kg ha^{-1} (SD: 150.7) for fish ≥2 cm, 79.7 kg ha^{-1} (SD: 131.1) for fish ≥4 cm and 68.3 kg ha^{-1} (SD: 109.1) for fish ≥8 cm, and biomass ranged between 1.3 and 318.2 kg ha^{-1} (only lakes with a Sawada index $N_v < 0.10$). Depth strata–specific fish biomass ranged between 0 and 378.3 kg ha^{-1}. There was a tendency towards higher fish biomass in the shallow strata relative to deep depth strata, although not as strong as observed in the gillnet catches. Particularly in deep lakes, a comparatively high fish biomass was observed at depths down to 35 m. A high Sawada index ($N_v > 0.10$) was found in three lakes (Nordborg, Loweswater and Rostherne Mere) after applying a TS threshold of −58 dB (2-cm-long fish), but it remained high in only one lake (Nordborg) after the TS threshold was raised to −52 dB (4-cm-long fish) (Table 3). However, removal of these lakes from the data set did not significantly influence the correlation strength, and therefore, we kept all lakes in the analyses. Furthermore, N_v was not influenced by the use of different sound frequencies (GLM: $t = -1.58$; $P = 0.14$) or pulse durations in our data set (GLM: $t = -1.27$; $P = 0.22$), suggesting unbiased comparison of the hydroacoustically obtained fish biomass estimates.

Comparison hydroacoustics – gillnet BPUE

We found a highly significant overall correlation between total S_v and BPUE across the 18 lakes ($r = 0.80$, $P < 0.001$; Fig. 2) with similar correlation strengths for all fish length thresholds tested ($r = 0.77$–0.80, $n = 18$, all $P < 0.001$; Table 3). When split into five successive depth strata (0–2.99 m, 3–5.99 m, 6–11.99 m, 12–19.99 m, 20–34.99 m), we found a significant correlation between S_v and BPUE for the shallowest strata for all fish length thresholds (Table 3). In stratum 3 (6–11.99 m), a significant correlation was only observed if fish echoes from fish <8 cm TL were ignored. In deeper strata (≥12 m), S_v was not at all correlated with BPUE (all $P > 0.47$). These results indicate that length thresholds had no impact on the correlation, whereas lake depth contributed substantially to the overall correspondence between the two types of sampling gear.

The importance of lake depth was confirmed when the reflected fish echo energy was converted into areal fish biomass (kg ha^{-1}). The OLS regression between gillnet

Table 3 Correlation between the log (x + 1)-transformed mean volumetric backscattering strength (S_v in dB) and log (x + 1)-transformed catches from benthic multi-mesh gillnets [BPUE (kg net^{-1} night^{-1})] for five depth strata and the total lake. Depth strata were defined according to the European standard for sampling fish in lakes with multi-mesh gillnets. Given are target strength (TS) and S_v thresholds and the corresponding range of fish lengths (LR) included in the analyses, Pearson's correlation coefficient (r) and the corresponding P-value. Significant correlations ($P \leq 0.05$) are highlighted in boldface

TS/S_v thresholds (dB)	LR (cm)	Depth stratum	r	P
−58/−64	2–∞	1*	**0.714**	**<0.001**
		2*	**0.681**	**0.002**
		3*	0.405	0.095
		4	0.182	0.550
		5	−0.226	0.666
		Total*	**0.797**	**<0.001**
−52/−58	4–∞	1	**0.753**	**<0.001**
		2	**0.654**	**0.003**
		3 *	0.430	0.074
		4	0.217	0.474
		5	−0.224	0.668
		Total	**0.788**	**<0.001**
−47/−53	8–∞	1	**0.749**	**<0.001**
		2	**0.624**	**0.006**
		3	**0.482**	**0.043**
		4	0.195	0.522
		5	−0.187	0.720
		Total	**0.774**	**<0.001**
−47/−53	8–60	1	**0.753**	**<0.001**
		2	**0.631**	**0.005**
		3	**0.592**	**0.010**
		4	0.182	0.551
		5	−0.187	0.720
		Total	**0.769**	**<0.001**

The number of lakes included in the correlation analyses was 18 (depth strata 1–3), 12 (depth stratum 4) and 6 (depth stratum 5).
*Indicate analyses where lakes with a Sawada index $N_v > 0.10$ were included.

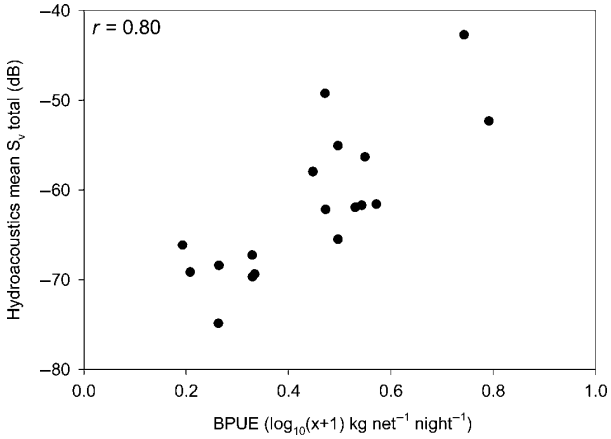

Fig. 2 Scatter plot of log(x + 1)-transformed benthic multi-mesh gillnet catches (kg net^{-1} night^{-1}) and mean total volumetric backscattering strength [S_v in decibel (dB)] from hydroacoustics for 18 European lakes. The correlation was highly significant (Pearson's $r = 0.80$; $P < 0.001$). The used target strength (TS)/S_v threshold was −52/−58 dB, which corresponds to fish ≥2 cm according to Love's equation (1971).

BPUE and areal fish biomass derived from hydroacoustics was not significant ($r^2 = 0.19$, $F = 3.82$, $P = 0.07$, $n = 18$). However, OLS became significant if the three very deep lakes were excluded (y = 3.697 x–0.198, $r^2 = 0.52$, $F = 14.18$, $P = 0.002$, $n = 15$, Fig. 3a). The intercept of this OLS (−0.198) did not differ from zero ($t = -0.40$, $P = 0.70$). A gillnet BPUE of 2 kg net^{-1} night^{-1} corresponds to a fish biomass of 36.8 kg ha^{-1}. However, for gillnet catches >6 kg net^{-1} night^{-1}, area-related fish biomass derived from the regression line was very high (>840 kg ha^{-1}).

If gillnet catches and hydroacoustics data were limited to the upper two strata (0–5.99 m), the OLS regression was significant as well (y = 4.090 x–0.896, $r^2 = 0.66$, $F = 31.14$, $P < 0.001$, $n = 18$). In this case, the deepest lakes did not deviate from the overall regression line (Fig. 3b). The intercept was significantly different from zero ($t = -2.16$, $P = 0.05$). A gillnet BPUE of 2 kg net^{-1} night^{-1} corresponds to a fish biomass of 11.4 kg ha^{-1} for the shallow depth stratum. At high gillnet catches (>7 kg net^{-1} night^{-1}), area-related fish biomass derived from the regression model was again very high (> 620 kg ha^{-1}).

Discussion

To our knowledge, our study is the first to show a strong significant correlation between gillnet catch data and fish biomass estimates obtained by hydroacoustics collected from a series of lakes varying strongly in morphometry and trophic status. By applying entire lakes as sample units, we found a strong log-linear correspondence between backscattered echo energy (S_v) from fish and average biomass caught by the gillnets (kg fish net^{-1} night^{-1}). After converting the reflected fish echo energy into areal fish biomass (kg ha^{-1}), the significant relationship with gillnet BPUE persisted if the three very deep lakes were excluded. The strength of correlations was independent of the fish length thresholds applied, but varied across the different depth strata of the lakes.

The observed discrepancy in correlation strength between the use of S_v and converted areal fish biomass demonstrates complications arising from conversion of the echo target strength into fish total length and the further conversion of fish length into fish biomass. These

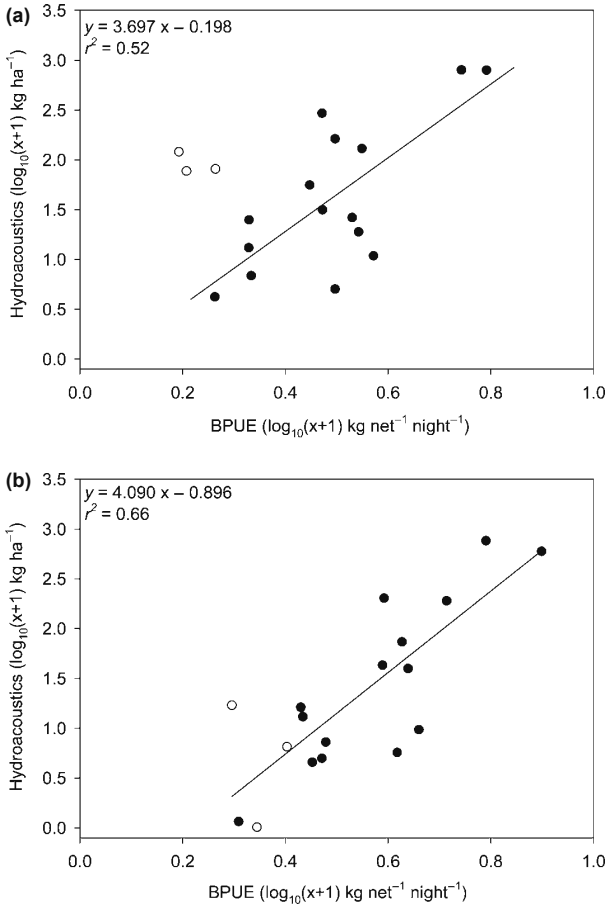

Fig. 3 Scatter plots and ordinary least-square regression lines between log(x + 1)-transformed benthic multi-mesh gillnet catches (kg net^{-1} night^{-1}) and log(x + 1)-transformed areal fish biomass (kg ha^{-1}) derived from hydroacoustics for the entire depth range analysed (surface to bottom; a) and for the upper depth stratum (0–6 m; b). The three deepest lakes (white circles) were excluded from the regression analysis for the entire depth range (a), but remained in the analysis of the shallow depth stratum (b). Given are the regression equation and the coefficient of determination (r^2). The used target strength (TS)/S_v threshold was −52/−58 dB, which corresponds to fish ≥2 cm according to Love's equation (1971).

calculations include two steps of uncertainty, particularly regarding large fish echoes. Typically, abundances of large fish are low, such that the few large fish echoes do not contribute substantially to the total backscattered echo energy. However, the conversion of S_v into a biological unit (kg fish ha^{-1}) can produce high fish biomass estimates from the few large fish because their SEDs contribute to the S_v scaling. The occurrence of a few very large fish can be detected by hydroacoustics, but may go undetected by gillnets (Psuty & Borowski, 1997), thereby weakening the relationship between the hydroacoustic estimates of fish biomass and gillnet BPUE.

According to the results of earlier studies, correspondence of fish abundance estimates between gillnets and hydroacoustics generally seemed weak (Peltonen *et al.*, 1999; Dennerline *et al.*, 2012), particularly in deep lakes (Jurvelius *et al.*, 2011; Achleitner *et al.*, 2012). However, these studies compared fish catches by gillnets with hydroacoustically obtained fish densities in single lakes where fish catches between individual nets can be highly variable both horizontally (area) and vertically (depth) (Prchalová *et al.*, 2009a; Deceliere-Vergès *et al.*, 2009) or they sampled fish assemblages by different gears at different seasons where different fish assemblages might be sampled by both gears (Winfield, Fletcher & James, 2007; Bobori & Salvarina, 2010). Therefore, combination of data from several gillnets and hydroacoustic transects sampled at short time intervals and by considering the entire lake as a sample unit, as in our study, reduces the effect of high temporal and spatial variability of fish samplings and thus substantially improves between-lake comparability.

Nevertheless, the strength of correspondence between the two types of gear declined in the deeper strata of the lakes. However, although the power of the statistical correlation was reduced for these analyses owing to the smaller sample sizes (12 and 6 lakes, respectively), we suggest that the weaker correspondence was primarily the result of less precise biomass estimates of pelagically living fish from benthic gillnets (*cf.* Deceliere-Vergès *et al.*, 2009; Achleitner *et al.*, 2012). At low productivity, the hypolimnion of European stratified lakes is occupied by stenothermic coldwater species of the order Salmoniformes (Beier, 2001; Guillard *et al.*, 2006; Mehner *et al.*, 2007a). The majority of these species are truly pelagic, although a few have benthic morphs (Kahilainen *et al.*, 2011). Therefore, they are underrepresented in benthic multi-mesh gillnet catches (Deceliere-Vergès & Guillard, 2008), and their relative abundance estimates from pelagic gillnets are less accurate even if the sampling effort is higher than a single vertical row of pelagic nets per lake according to the CEN standard (Achleitner *et al.*, 2012). However, these fish are reliably detected by vertical hydroacoustics, because the sound transmitted and hence the volume of water sampled increase with increasing water depth. Precision of biomass estimates is even higher by conducting night-time hydroacoustics because many pelagic fish perform diurnal vertical migration and disperse more evenly in the pelagic area at night (Appenzeller & Leggett, 1992; Mehner *et al.*, 2007b).

In contrast, fish biomass in shallow or highly productive deep lakes is highest in strata close to the surface, particularly if environmental conditions at greater depths

are less favourable for the fish population (Draštík *et al.*, 2009). Consequently, the highest fish catches by multi-mesh gillnets usually appear in the upper depth strata (Lauridsen *et al.*, 2008; Prchalová *et al.*, 2009a; this study). The ratio between the open water and near-benthic volume of these lakes is often low; hence, catches in benthic gillnets are representative for the fish assemblage in these strata. Furthermore, diurnal horizontal migrations of fish between onshore and offshore shallow strata (Lewin, Okun & Mehner, 2004; Pekcan-Hekim *et al.*, 2005) are covered by gillnet catches because the nets are set overnight and there catch the fish during their migration and activity peaks at dusk and dawn (Prchalová *et al.*, 2010). Nevertheless, the very strong correspondence between hydroacoustically and gillnet-derived fish biomass particularly for the shallow depth strata was not expected, since previous studies have revealed that vertical, downward-looking hydroacoustics underestimates fish abundance in shallow waters (Knudsen & Sægrov, 2002; Draštík *et al.*, 2009). For example, in two of the study lakes, no fish >8 cm were detected by hydroacoustics in the upper depth strata, whereas a few individuals were caught by gillnets. Accordingly, the negative regression intercept for fish biomass estimates from the shallow depth strata (0–5.99 m) was significantly different from zero, indicating that fish biomass in these strata may be underestimated by vertical hydroacoustics even after adding fish biomass from the layer beyond the near-field dead zone of the transducers (2–3 m) to the upper blind zone (0–2 m). However, our data also indicate that if fish are more abundant, vertical hydroacoustics can produce fish biomass estimates that strongly correspond with benthic gillnet catches, even for shallow lake depth strata.

Earlier studies have suggested that correspondence between hydroacoustics and gillnet-derived fish abundances can be improved if analyses are limited to the size range of fish that both gears sample efficiently (Mehner & Schulz, 2002; Dennerline *et al.*, 2012). In general, acoustic fish length distributions are wider than those obtained by net fishing gears (Emmrich *et al.*, 2010; Jurvelius *et al.*, 2011). Consequently, removal from the analysis of fish from the lower and upper end of the size spectrum might improve the comparability and correspondence of fish abundance estimates (Mehner & Schulz, 2002). In our analyses, however, application of varying fish size thresholds did not significantly affect the results. Although numerical dominance of small, newly hatched fish may characterise fish assemblages in lakes during spring and summer, intermediate-sized fish are dominant in late summer/early autumn, when sampling took place, owing to reduced abundance of small fish by growth and high mortality over the seasons. Consequently, based on our hydroacoustic observations, fish of 2- to 4-cm total length which are most likely one-summer-old recruits contributed on average only 12.2% to the total biomass. Likewise, very large fish contributed on average only 5% to the standing biomass because of their low overall abundance. These calculations further indicate that total biomass of fish is a less variable descriptor than numerical abundance for lake fish assemblages. Accordingly, correspondence between gears is usually stronger in biomass comparisons (Mehner *et al.*, 2003; Emmrich *et al.*, 2010). This is no limitation since information on trophic interactions and energy budgets of lakes requires biomass estimates of trophic variables (Jeppesen *et al.*, 1998), and the correspondence between trophic state or productivity of lakes and their fish assemblages is usually also stronger for biomass than for abundance units (Hanson & Leggett, 1982; Garcia *et al.*, 2006).

Although our data fit best to linear models, the general log-linear relationship between gillnet CPUE and absolute fish biomass may become biased at very high fish densities (Linløkken & Haugen, 2006; Prchalová *et al.*, 2011). Maximum catch capacity of the standardised benthic multi-mesh gillnets has been estimated to 11 kg net^{-1} (Prchalová *et al.*, 2011). During our samplings, only three of 455 nets caught more than 10 kg fish, suggesting that our gillnet catch data were not strongly biased by saturation effects. However, we cannot exclude the possibility that the linear pattern might change if more lakes with very high fish densities are included. Our regression lines for the prediction of fish biomass from relative gillnet catches also suggested reduced reliability at high fish densities, because an average gillnet catch of >6 kg net^{-1} night^{-1} predicts areal fish biomasses >600 kg ha^{-1} which are rarely observed in stratified natural European lakes.

The results of our comparative approach are encouraging and support the more frequent application of vertical hydroacoustics for the quantification of fish biomass in stratified lakes. Survey designs combining hydroacoustics and limited gillnetting at sampling dates with short time intervals, the latter for inventory sampling only (i.e. apportionment of species data from gillnet catches to hydroacoustic data) rather than CPUE calculations, offer a cost-effective strategy for sampling lake fish assemblages. This approach is particularly appropriate because gillnetting can create ethical problems or conflicts with interests of local recreational fisheries.

In turn, standardised gillnet sampling by benthic nets in moderately deep lakes may be used to roughly predict

areal fish biomasses according to our regression equations. Whether the equation derived for the upper depth strata can be applied to shallow, polymictic lakes as well deserves further studies. Furthermore, gillnet sampling seems not to provide sufficiently reliable relative fish density estimates in very deep lakes with separate, pelagic-dwelling fish assemblages irrespective of whether the full set of benthic nets is used or is supplemented with pelagic nets required to sample fish in deep lakes (>10 m maximum depth) even if the sampling effort is higher than proposed by the European gillnet standard EN14757 (CEN, 2005; Deceliere-Vergès & Guillard, 2008; Achleitner *et al*., 2012). To comply with the requirement for quantitative information on pelagic lake fish assemblages (Lauridsen *et al*., 2008), representative sampling should be conducted using active sampling gears that are more efficient and give more accurate estimates on fish abundance (Haakana & Huuskonen, 2008; Jurvelius *et al*., 2011). It has already been demonstrated that catches from these gears are comparable to those obtained by hydroacoustics if sampling systems are sufficiently developed (Emmrich *et al*., 2010).

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References

Achleitner D., Gassner H. & Luger M. (2012) Comparison of three standardised fish sampling methods in 14 alpine lakes in Austria. *Fisheries Management & Ecology*, **19**, 352–361.

Aglen A. (1983) Random errors of acoustic fish abundance estimates in relation to the survey grid density applied. *FAO Fisheries Report*, **300**, 293–298.

Appelberg M., Berger H.M., Hesthagen T., Kleiven E., Kurkilahti M., Raitaniemi J. *et al.* (1995) Development and intercalibration of methods in Nordic freshwater fish monitoring. *Water Air and Soil Pollution*, **85**, 401–406.

Appenzeller A.R. & Leggett W.C. (1992) Bias in hydroacoustic estimates of fish abundance due to acoustic shadowing - evidence from day night surveys of vertically migrating fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2179–2189.

Balk H. & Lindem T. (2011) Sonar4 and Sonar5-Pro post processing systems. *Operator manual version* **6.01**.

Beier U. (2001) Habitat distribution and size structure in freshwater fish communities: effects of vendace on interactions between perch and roach. *Journal of Fish Biology*, **59**, 1437–1454.

Bethke E., Arrhenius F., Cardinale M. & Hakansson N. (1999) Comparison of the selectivity of three pelagic sampling trawls in a hydroacoustic survey. *Fisheries Research*, **44**, 15–23.

Bobori D.C. & Salvarina I. (2010) Seasonal variation of fish abundance and biomass in gillnet catches of an East Mediterranean lake: Lake Doirani. *Journal of Environmental Biology*, **31**, 995–1000.

CEN (European Committee for Standardisation) (2005) *EN 14757. Water Quality – Sampling of Fish with Multi-mesh Gillnets, Brussels*. CEN, Brussels.

Dahm E., Hartmann J., Jurvelius J., Loffler H. & Volzke V. (1992) Review of the European-Inland-Fisheries-Advisory-Commission (Eifac) experiments on stock assessment in lakes. *Journal of Applied Ichthyology*, **8**, 1–9.

Deceliere-Vergès C., Argillier C., Lanoiselée C., De Bortoli J. & Guillard J. (2009) Stability and precision of the fish metrics obtained using CEN multi-mesh gillnets in natural and artificial lakes in France. *Fisheries Research*, **99**, 17–25.

Deceliere-Vergès C. & Guillard J. (2008) Assessment of the pelagic fish populations using CEN multi-mesh gillnets: consequences for the characterization of the fish communities. *Knowledge and Management of Aquatic Ecosystems*, **389**, 04.

Dennerline D.E., Jennings C.A. & Degan D.J. (2012) Relationships between hydroacoustic derived density and gill net catch: Implications for fish assessments. *Fisheries Research*, **123–124**, 78–89.

Diekmann M., Brämick U., Lemcke R. & Mehner T. (2005) Habitat-specific fishing revealed distinct indicator species in German lowland lake fish communities. *Journal of Applied Ecology*, **42**, 901–909.

Draštík V., Kubečka J., Čech M., Frouzová J., Říha M., Jůza T. *et al.* (2009) Hydroacoustic estimates of fish stocks in temperate reservoirs: day or night surveys? *Aquatic Living Resources*, **22**, 69–77.

Elliott J.M. & Fletcher J.M. (2001) A comparison of three methods for assessing the abundance of Arctic charr, *Salvelinus alpinus*, in Windermere (northwest England). *Fisheries Research*, **53**, 39–46.

Emmrich M., Helland I.P., Busch S., Schiller S. & Mehner T. (2010) Hydroacoustic estimates of fish densities in comparison with stratified pelagic trawl sampling in two deep, coregonid-dominated lakes. *Fisheries Research*, **105**, 178–186.

European Union (2000) Directive 2000/60EC of the European Parliament and of the Council of Establishment a framework of the community action in the field of water policy. European Commission. *Official Journal of the European Communities*, **327**, 1.

Garcia X.F., Diekmann M., Brämick U., Lemcke R. & Mehner T. (2006) Correlations between type-indicator fish species and lake productivity in German lowland lakes. *Journal of Fish Biology*, **68**, 1144–1157.

Godlewska M., Colon M., Doroszczyk L., Długoszewski B., Verges C. & Guillard J. (2009) Hydroacoustic measurements at two frequencies: 70 and 120 kHz – consequences for fish stock estimation. *Fisheries Research*, **96**, 11–16.

Godlewska M., Colon M., Jóźwik A. & Guillard J. (2011) How pulse lengths impact fish stock estimations during hydroacoustic measurements at 70 kHz. *Aquatic Living Resources*, **24**, 71–78.

Guillard J., Lebourges-Dhaussy A. & Brehmer P. (2004) Simultaneous Sv and TS measurements on Young-of-the-Year (YOY) freshwater fish using three frequencies. *ICES Journal of Marine Science*, **61**, 267–273.

Guillard J., Perga M.E., Colon M. & Angeli N. (2006) Hydroacoustic assessment of young-of-year perch, *Perca fluviatilis*, population dynamics in an oligotrophic lake (Lake Annecy, France). *Fisheries Management and Ecology*, **13**, 319–327.

Haakana H. & Huuskonen H. (2008) Effects of intensive fishing on the perch population in a large oligotrophic lake in eastern Finland. *Fisheries Research*, **91**, 144–150.

Hamley J.M. (1975) Review of gillnet selectivity. *Journal of the Fisheries Research Board of Canada*, **32**, 1943–1969.

Hanson J.M. & Leggett W.C. (1982) Empirical prediction of fish biomass and yield. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 257–263.

Harrison A.J., Kelly F.L., Rosell R.S., Champ T.W.S., Connor L. & Girvan J.R. (2010) First record and initial hydroacoustic stock assessment of Pollan *Coregonus autumnalis* PALLAS in Lough Allen, Ireland. *Biology & Environment: Proceedings of the Royal Irish Academy*, **110**, 69–74.

Helland I.P., Freyhof J., Kasprzak P. & Mehner T. (2007) Temperature sensitivity of vertical distributions of zooplankton and planktivorous fish in a stratified lake. *Oecologia*, **151**, 322–330.

Jackson D.A. & Harvey H.H. (1997) Qualitative and quantitative sampling of lake fish communities. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 2807–2813.

Jeppesen E., Søndergaard M., Jensen J.P., Mortensen E., Hansen A.-M. & Jørgensen T. (1998) Cascading trophic interactions from fish to bacteria and nutrients after reduced sewage loading: an 18-year study of a shallow hypertrophic lake. *Ecosystems*, **1**, 250–267.

Jurvelius J., Kolari I. & Leskelä A. (2011) Quality and status of fish stocks in lakes: gillnetting, seining, trawling and hydroacoustics as sampling methods. *Hydrobiologia*, **660**, 29–36.

Kahilainen K., Siwertsson A., Gjelland K., Knudsen R., Bøhn T. & Amundsen P.A. (2011) The role of gill raker number variability in adaptive radiation of coregonid fish. *Evolutionary Ecology*, **25**, 573–588.

Knudsen F.R., Larsson P. & Jakobsen P.J. (2006) Acoustic scattering from a larval insect (*Chaoborus flavicans*) at six echosounder frequencies: Implication for acoustic estimates of fish abundance. *Fisheries Research*, **79**, 84–89.

Knudsen F.R. & Sægrov H. (2002) Benefits from horizontal beaming during acoustic survey: application to three Norwegian lakes. *Fisheries Research*, **56**, 205–211.

Kubečka J., Godø O.R., Hickley P., Prchalová M., Říha M., Rudstam L. *et al*. (2012) Fish sampling with active methods. *Fisheries Research*, **12**, 3–124.

Kubečka J., Hohausova E., Matena J., Peterka J., Amarasinghe U.S., Bonar S.A. *et al*. (2009) The true picture of a lake or reservoir fish stock: a review of needs and progress. *Fisheries Research*, **96**, 1–5.

Lauridsen T.L., Landkildehus F., Jeppesen E., Jorgensen T.B. & Søndergaard M. (2008) A comparison of methods for calculating Catch Per Unit Effort (CPUE) of gill net catches in lakes. *Fisheries Research*, **93**, 204–211.

Legendre P. & Legendre L. (1998) *Numerical Ecology, 2nd English edn*. Elsevier, Amsterdam.

Lewin W., Okun N. & Mehner T. (2004) Determinants of the distribution of juvenile fish in the littoral area of a shallow lake. *Freshwater Biology*, **49**, 410–424.

Linløkken A. & Haugen T.O. (2006) Density and temperature dependence of gill net catch per unit effort for perch, *Perca fluviatilis*, and roach, *Rutilus rutilus*. *Fisheries Management and Ecology*, **13**, 261–269.

Love R.H. (1971) Dorsal-aspect target strength of an individual fish. *Journal of the Acoustical Society of America*, **49**, 1397–1403.

Mehner T., Gassner H., Schulz M. & Wanzenböck J. (2003) Comparative fish stock estimates in Lake Stechlin by parallel split-beam echosounding with 120 kHz. *Archiv für Hydrobiologie Special Issues Advances in Limnology*, **58**, 227–236.

Mehner T., Holmgren K., Lauridsen T.L., Jeppesen E. & Diekmann M. (2007a) Lake depth and geographical position modify lake fish assemblages of the European 'Central Plains' ecoregion. *Freshwater Biology*, **52**, 2285–2297.

Mehner T., Kasprzak P. & Hölker F. (2007b) Exploring ultimate hypotheses to predict diel vertical migrations in coregonid fish. *Canadian Journal of Fisheries and Aquatic Sciences*, **64**, 874–886.

Mehner T. & Schulz M. (2002) Monthly variability of hydroacoustic fish stock estimates in a deep lake and its correlation to gillnet catches. *Journal of Fish Biology*, **61**, 1109–1121.

Olin M., Kurkilahti M., Peitola P. & Ruuhijärvi J. (2004) The effects of fish accumulation on the catchability of multimesh gillnet. *Fisheries Research*, **68**, 135–147.

Olin M., Malinen I. & Ruuhijärvi J. (2009) Gillnet catch in estimating the density and structure of fish community-Comparison of gillnet and trawl samples in a eutrophic lake. *Fisheries Research*, **96**, 88–94.

Parker-Stetter S.L., Rudstam L.G., Sullivan P.J. & Warner D.M. (2009) *Standard Operating Procedures for Fisheries Acoustic Surveys in the Great Lakes*. Great Lakes Fisheries Commission Special Publication, Ann Arbor, 09-01.

Pekcan-Hekim Z., Horppila J., Nurminen L. & Niemistö J. (2005) Diel changes in habitat preference and diet of perch (*Perca fluviatilis*), roach (*Rutilus rutilus*) and white bream (*Abramis bjoerkna*). *Archiv für Hydrobiologie Special Issues Advances in Limnology*, **59**, 173–187.

Peltonen H., Ruuhijärvi J., Malinen T. & Horppila J. (1999) Estimation of roach (*Rutilus rutilus* (L.)) and smelt (*Osmerus eperlanus* (L.)) stocks with virtual population analysis, hydroacoustics and gillnet CPUE. *Fisheries Research*, **44**, 25–36.

Prchalová M., Kubečka J., Čech M., Frouzová J., Draštík V., Hohausová E. *et al.* (2009a) The effect of depth, distance from dam and habitat on spatial distribution of fish in an artificial reservoir. *Ecology of Freshwater Fish*, **18**, 247–260.

Prchalová M., Kubečka J., Říha M., Mrkvička T., Vašek M., Jůza T. *et al.* (2009b) Size selectivity of standardized multimesh gillnets in sampling coarse European species. *Fisheries Research*, **96**, 51–57.

Prchalová M., Mrkvička T., Kubečka J., Peterka J., Čech M., Muška M. *et al.* (2010) Fish activity as determined by gillnet catch: A comparison of two reservoirs of different turbidity. *Fisheries Research*, **102**, 291–296.

Prchalová M., Mrkvička T., Peterka J., Čech M., Berec L. & Kubečka J. (2011) A model of gillnet catch in relation to the catchable biomass, saturation, soak time and sampling period. *Fisheries Research*, **107**, 201–209.

Psuty I. & Borowski W. (1997) The selectivity of gill nets to bream (*Abramis brama* L.) fished in the Polish part of the Vistula Lagoon. *Fisheries Research*, **32**, 249–261.

R Development Core Team (2009) *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Wien. Available from http://www.R-project.org.

Sawada K., Furusawa M. & Williamson N.J. (1993) Condition for the precise measurement of fish target strength *in situ*. *Journal of the Marine Acoustical Society of Japan*, **20**, 73–79.

Simmonds J. & MacLennan D. (2005) *Fisheries Acoustics: Theory and Practice*. 2nd edn. Blackwell Science. Oxford. *Fish and Aquatic Resources Series* 10.

Søndergaard M., Jeppesen E., Jensen J.P. & Amsinck S.L. (2005) Water framework directive: ecological classification of Danish lakes. *Journal of Applied Ecology*, **42**, 616–629.

Van Den Avyle M.J., Boxrucker J., Michaletz P., Vondracek B. & Ploskey G.R. (1995) Comparison of catch rate, length distribution, and precision of six gears used to sample reservoir shad populations. *North American Journal of Fisheries Management*, **15**, 940–955.

Wanzenböck J., Mehner T., Schulz M., Gassner H. & Winfield I.J. (2003) Quality assurance of hydroacoustic surveys: the repeatability of fish-abundance and biomass estimates in lakes within and between hydroacoustic systems. *ICES Journal of Marine Science*, **60**, 486–492.

Winfield I.J., Emmrich M., Guillard J., Mehner T. & Rustadbakken A. (2011) Guidelines for standardisation of hydroacoustic methods. WISER deliverable 3.4-3. Available from http://www.wiser.eu/download/D3.4-3.pdf [accessed 10 April 2012].

Winfield I.J., Fletcher J.M. & James J.B. (2007) Seasonal variability in the abundance of Arctic charr (*Salvelinus alpinus* (L.)) recorded using hydroacoustics in Windermere UK and its implications for survey design. *Ecology of Freshwater Fish*, **16**, 64–69.

Winfield I.J., Fletcher J.M., James J.B. & Bean C.W. (2009) Assessment of fish populations in still waters using hydroacoustics and survey gill netting: Experiences with Arctic charr (*Salvelinus alpinus*) in the UK. *Fisheries Research*, **96**, 30–38.

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Paper III

Emmrich, **M.**, Helland, I.P., Busch, S., Schiller, S., and Mehner, T.

Hydroacoustic estimates of fish densities in comparison with stratified pelagic trawl sampling in two deep, coregonid-dominated lakes

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Hydroacoustic estimates of fish densities in comparison with stratified pelagic trawl sampling in two deep, coregonid-dominated lakes

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ABSTRACT

Reliable information on fish stocks is given crucial importance in fisheries science and ecosystem management. Among others, the European Water Framework Directive calls for consistent sampling methods that provide comparable and reproducible results. However, the standardized sampling of fish in lakes by gillnets is conducted by low effort only in the pelagic areas, thus potentially not reflecting between-lake variability in fish density. Here, we compared two additional fishing methods, hydroacoustics and mid-water trawl sampling, to estimate pelagic coregonid densities in two deep lakes. Night-time trawling was conducted in four different depth layers and compared with the simultaneously obtained abundance and biomass estimates from echo recordings. Overall areal fish biomass from both methods corresponded to each other ($R^2 = 0.40$), with slope and intercept of major axis regression not differing from unity. However, we found differences in estimates for the deepest layers fished, and for very small and the largest coregonids, most likely to be explained by the specific technological details of either method. Our study supports that either hydroacoustics or trawl sampling should accompany gillnet fishing to monitor pelagic fish assemblages. Because both methods result in estimates of absolute fish densities per volume or area, their application may uncover subtle responses of fish assemblages to anthropogenic disturbance in deep lakes.

1. Introduction

Reliable information on fish stocks is given crucial importance in fisheries science and ecosystem management (Cowx, 1996; Hoggarth et al., 2006). Consequently, this demand promotes a continuous improvement of survey designs including application of various gears for freshwater fish sampling (Appelberg et al., 1995; Frouzova et al., 2005; Adams et al., 2006; Guillard and Vergès, 2007). A combination of different gears seems to be most promising to gain a 'true picture' of lake fish stocks, in particular if several gears produce similar results from the same habitat (Kubečka et al., 2008).

The European Water Framework Directive (WFD; 2000/60/EC) calls for consistent sampling methods that provide comparable and reproducible results. According to the protocol EN 14757 (European Committee for Standardization (CEN), 2005), lakes have to be sampled with benthic multi-mesh gillnets. The fishing effort of this stratified sampling design increases systematically with lake depth and area. Lakes exceeding maximum depths of 10 m should additionally be sampled with only one row of pelagic gillnets placed over the deepest location. The effort of pelagic gillnet sampling is fixed and hence independent of lake morphometry. Accordingly, the voluminous hypolimnetic areas of deep lakes are poorly covered by the standardized gillnet sampling schemes (Deceliere-Vergès and Guillard, 2008).

The pelagic habitats of European temperate deep lakes are usually dominated by fish species of the order Salmoniformes (charr, *Salvelinus* spp.; trout, *Salmo* spp.; coregonids, *Coregonus* spp.) (Persson et al., 1991; Beier, 2001; Mehner et al., 2007a). These sensitive species display indicator functions, as they are most vulnerable to environmental degradations (Müller, 1992; Rask et al., 2010). The numerical proportion of pelagic fish often by far exceeds the contribution of littoral and profundal species to the lake-wide fish abundance (Deceliere-Vergès and Guillard, 2008). Consequently, adequate sampling of the pelagic areas is needed in particular when evaluating the ecological integrity of deep lakes based on their fish assemblages.

Hydroacoustics and sampling by active gear, for example trawls, are potential additional methods to monitor pelagic fish assemblages (Jurvelius et al., 2005; Simmonds and MacLennan, 2005; Doroszczyk et al., 2007; Schmidt et al., 2005; Kubečka et al., 2008). However, trawling is still less frequently applied in freshwater fish-

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ery science, as it is associated with relatively high sampling effort and requests sophisticated equipment.

Combined surveys of hydroacoustics and pelagic trawling may offer extended information on fish abundances and biomass (Argyle, 1992), because both methods complement each other by balancing their individual drawbacks. Hydroacoustics provide the most comprehensive data sets on pelagic fish densities (Elliott and Fletcher, 2001) including a general view of the overall existing size spectrum (Coll et al., 2007). In contrast, trawling provides information on the fish stock's species composition and length distribution (Bethke et al., 1999). However, the correspondence between fish densities obtained by either hydroacoustics or pelagic trawling is usually poor (Jurvelius et al., 2005; Mason et al., 2005; Stockwell et al., 2007). Therefore, it remains questionable whether the methods can substitute each other if financial or technological constraints prevent their simultaneous application.

Here, we tested if hydroacoustics and pelagic trawling results in comparable fish densities if operated in lakes whose pelagic fish assemblages are dominated only by coregonids. Coregonids are the most frequently occurring pelagic species in deep, nutrient-poor lakes of Central and North Europe (Mehner et al., 2007a). In general, coregonid species disperse from dense aggregations at daytime into nearly stochastic spatial distributions within the pelagic layers at night (e.g. *Coregonus albula* (L.): Świerzowski, 2001; Schmidt et al., 2005, *Coregonus lavaretus* (L.): Gjelland et al., 2009, *Coregonus hoyi* (Milner): Brandt et al., 1991, *Coregonus artedi* Lesueur: Milne et al., 2005). This behaviour makes them both easily detectable as single echoes by night-time hydroacoustics and directly accessible to night-time trawl sampling. We included hydroacoustic data and concurrent trawl catches from 16 night-time surveys, sampled in two deep lakes with differing trophic levels over four years. The aim was to compare density estimates from hydroacoustics and trawl samples with respect to sampling depth and size of fish caught. Furthermore, we evaluated whether a similar lake-wide estimate of pelagic fish biomass can be obtained by both sampling approaches.

2. Methods

2.1. Study area

Our study was conducted at Lakes Stechlin and Breiter Luzin. Lake Stechlin (53°10′ N; 13°02′ E) is an oligo-mesotrophic lake situated approximately 120 km north of Berlin, Germany. The deep (max. 69 m) dimictic lake has a mean depth of 22.8 m and a surface area of 430 ha. A total of 13 fish species inhabit the lake. The hypolimnetic fish community consists almost exclusively of European vendace (*C. albula* (L.)) and the endemic Fontane cisco (*Coregonus fontanae* Schulz & Freyhof) (Mehner and Schulz, 2002; Helland et al., 2007). Roach (*Rutilus rutilus* (L.)), bleak (*Alburnus alburnus* (L.)) and perch (*Perca fluviatilis* L.) occasionally occur in the epipelagic layers (Anwand et al., 2003).

Lake Breiter Luzin (53°20′ N; 13°28′ E), a mesotrophic lake of 345 ha with a maximum depth of 58.3 m (mean depth 22.3 m), is also inhabited by a species pair of coregonids. Vendace and the endemic cisco *Coregonus lucinensis* Thienemann dominate the pelagic community and coexist with a low number of other species, mainly perch, roach and bleak (Waterstraat et al., 2003).

2.2. Data sampling and analyses

Hydroacoustic data and catches from concurrent trawl hauls from 16 night-time surveys, conducted over four years and including ten months (see Appendix A), were incorporated in this study. All samplings started at least 90 min after sunset when fishes had dispersed in the pelagic layers.

2.2.1. Hydroacoustics

A SIMRAD EY-60 split beam echo sounder (SIMRAD; Kongsberg, Norway) operating at a frequency of 120 kHz was used during all surveys. The settings of the circular transducer (type ES 120-7C) with a nominal beam angle of $7^\circ \times 7^\circ$ were kept identical: pulse duration 256 μs, sample interval 0.047 m and receiver bandwidth 8.71 kHz. Pulse interval was set to 0.3 s and transects were recorded at a boat speed of 6 ± 0.81 km h^{-1} on average (±standard deviation (SD)). Depending on the mean water temperature, sound speed was adjusted according to the equation implemented in the SIMRAD software. Calibration was performed twice in 2005 and during each sampling campaign in the years 2006, 2008 and 2009 in accordance to the SIMRAD operator manual using a 23 mm standard copper sphere with reference target strength of −40.44 dB at 120 kHz. The hydroacoustic survey design consisted of five non-overlapping transects that crossed the deepest central and northern basins of Lake Stechlin and seven non-overlapping parallel transects crossing the deepest central part of Lake Breiter Luzin.

Echo recordings were stored on a computer and the files were later analyzed using the Sonar 5Pro software (version 5.9.7; Balk and Lindem, 2007). Only file segments exceeding 30 m water depth were included in the analyses which resulted in a cumulative transect length of 3 km on average for Lake Stechlin. In May 2005 and June 2009, only four transects (2.5 km) could be recorded due to technical problems. Cumulative transect length of Lake Breiter Luzin was 4 km on average.

For echo post-processing, transects were split into four layers of 5 m thickness each (opening height of the trawl ± 1 m) analogous to the towed trawl depths (see Fig. 1, Appendix A). Each layer was analyzed separately by converting the volumetric backscattering strength (S_v) into volumetric densities (D_{vol}: fish 1000 m^{-3}) and area densities (D_{area}: kg ha^{-1}). Additionally, we analyzed the fish density in the total pelagic volume from 10 m to 35 m depth to compare it with the interpolated catches of each trawl campaign (see Section 2.2.2, Fig. 1). To exclude distorting non-fish echoes (e.g. from air bubbles induced by wind), lower thresholds during post-processing were set to −66 dB S_v and −60 dB target strength (TS). TS frequency of single echo detection (SED) was categorized into four different size classes between −55 and −35 dB (step 5 dB), thus covering a fish length spectrum of 4–25 cm (Mehner, 2006). This length range reflects the minimum size that could be theoretically caught by the trawl and the maximum size of coregonids occurring in the two lakes observed in previous studies (Mehner and Schulz, 2002; Scharf, 2007). As almost 90% of all trawl catches exclusively consisted of coregonids, we assume that all pelagic fish echoes in the two lakes resulted from coregonids.

Fish-size determination of the detected single echoes was based on the specific TS-length regression for vendace: TS (dB) = 25.5 $\log_{10}$ (TL (cm)) −70.9 (Mehner, 2006).

2.2.2. Trawling

Concurrent trawling was carried out by a two-man crew on a separate boat (length 7 m, width 2 m) which was driven by a 60 hp outboard engine. The black-coloured midwater trawl has a total length of 14.8 m (stretched on land) with an opening area of approximately 10 m^2 (opening width 3.5 m) during towing process and mesh sizes of 28 mm (knot to knot) in the frontal part, 20 mm in the middle and 10 mm in the cod-end (further details see Fig. 2). Trawling speed (mean ± SD) was 6.5 ± 0.6 km h^{-1} (1.8 ± 0.2 m s^{-1}). Towed distance, as the product of trawling speed and trawling time, ranged between 500 m and 1600 m (mean 840 m) at Lake Stechlin and between 1000 m and 1900 m (mean 1400 m) at Lake Breiter Luzin. Towing time (±SD) was 7.8 min (±1.9) on average at Lake Stechlin and 13.3 min (±1.7) at Lake Breiter Luzin. Fishing was performed longitudinally in the deepest basins of both lakes, thus crossing the hydroacoustic transects. During each survey, four hauls

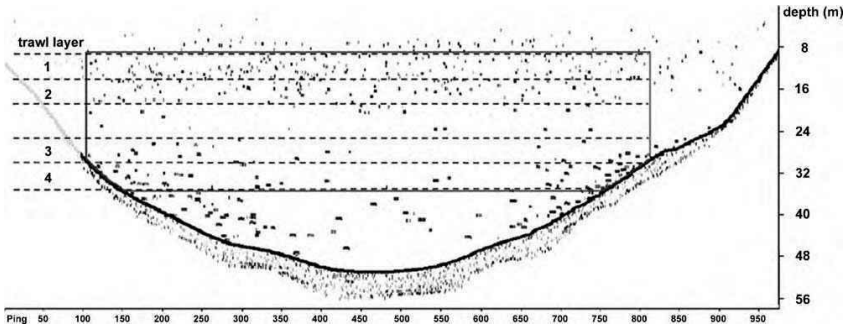

Fig. 1. Echogram (single-echo-detection mode) of the fish distribution in Lake Stechlin (June 2008). Solid lines border the analyzed pelagic volume (i.e. 10–35 m). Dashed lines represent the depths where trawling was conducted (layers of 5 m thickness; i.e. opening height of the trawl ± 1 m).

at different depths were performed separately at approximately 12 m, 15 m, 25 m and 32 m (mean ± SD: 12 ± 0.65 m, 15 ± 1.09 m, 25 ± 2.08 m and 32 ± 0.90 m). Deeper hauls could not be performed due to the limited spatial extension of water layers with more than 35 m depth. A diving computer mounted on the trawl's head rope recorded the actual sampling depth. The depth variability during each tow never exceeded 3 m. At the end of each haul, the trawl was quickly lifted by hydraulic winches at speeds comparable to the trawling speeds, thus preventing escapement of fish from the net. Due to technical problems, trawl data from 32 m depth in Lake Stechlin (August 2005) and data from 15 m trawl depth in Lake Breiter Luzin (April 2008) were missing.

Fishes were measured to the nearest millimetre (standard length (SL), TL or both) and weighed to the nearest gram wet mass (wm). Random subsamples of approximately 2 kg were processed from four big catches (from trawling depths 10–13 m and 14–17 m, Lake Breiter Luzin, 2008; 2009, see Appendix A) and their size compositions were extrapolated to the total catch. To standardize all length and weight data from the 16 sampling campaigns, we converted, if necessary, SL into TL using the regression formula for vendace: $TL = 1.206 \times SL - 0.429$ ($n = 933$, $R^2 = 0.99$). If fish weights were only incompletely recorded, the weights were calculated from lengths according to the length–weight regression: $W = 0.00507 \times TL^{3.089}$ (Mehner et al., 2003).

Volumetric fish densities (fish 1000 m^{-3}) were calculated by dividing the number of fishes caught during each haul by the towed volume of the trawl net (product of the towed distance and the opening area of the net). Areal biomass (kg ha^{-1}) was obtained by dividing the total weight of the catch by the product of the towed distance and the opening width (3.5 m) of the trawl net. To test if our trawling design provided pelagic biomass comparable to those from hydroacoustics, we interpolated the layer-specific trawl catches to the total pelagic volume (i.e. from 10 m to 35 m depth) by adding the calculated biomass from the adjacent layers in which trawling was conducted. In cases of slightly overlapping layers, biomass was subtracted analogously.

To analyze whether density estimates were sensitive to differing fish sizes, SEDs from hydroacoustics and trawl catches were split into four size groups: −55 to −50 dB (4–6.5 cm TL), −50 to −45 dB (>6.5–10 cm), −45 to −40 dB (>10–16 cm) and −40 to −35 dB (>16–25 cm). Furthermore, the total size-frequency distributions obtained from all fishes caught by the trawl (TL converted to TS) and all SEDs recorded by hydroacoustics were plotted. Mean length of fishes from SEDs were calculated from mean TS of each layer from all transects and converted into TL according to the equation of Mehner (2006).

2.3. Statistics

For an approximation to normal distribution and homoscedasticity, the density data were $\log_{10}$ or $\log_{10}(x+1)$ transformed. Subsequent one-sample Kolmogorov–Smirnov tests and Levene tests indicated normal distribution and homogeneity of variances ($P > 0.05$).

We used major axis regressions (MAR) to test for coherency between volumetric or areal densities of both sampling gears, because ordinary least-square regressions are not appropriate if both variables are estimated with an unknown error term (Legendre and Legendre, 1998). If a linear relationship was observed, depth-specific volumetric densities and areal densities of the different size classes were tested for common slopes and against the 1:1 fit (slope = 1, intercept = 0) which would indicate a perfect correspondence between hydroacoustic and trawling data. This procedure is in principal identical to the conventional ANCOVA that

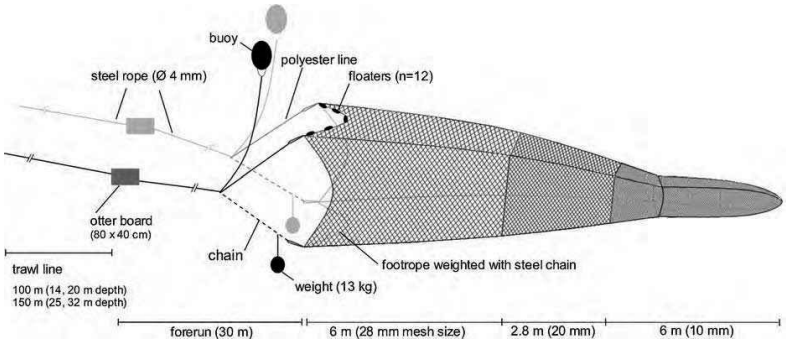

Fig. 2. Schematic view of the trawl net.

compares slopes and intercepts of ordinary least-square regressions. Total areal biomass (kg ha^{-1}) was also tested for differences in the slope and intercept against the 1:1 fit. For more statistical details of MAR see Warton et al. (2006).

To test for differences between the length–frequency distributions from hydroacoustics (SED) and trawling, we used the two-sample Kolmogorov–Smirnov test. All statistical calculations were performed using the R software (R Development Core Team Version 2.10, 2009) including the packages "lmodel2" (version 1.6.3) and "smatr" (version 2.1). The level of significance was set to $\alpha = 0.05$.

3. Results

In total 24,398 coregonids were caught during the trawl campaigns, and number of single echo detections (SED) for the total pelagic volume (10–35 m) was 231,975. Overall areal fish biomass in the pelagic area (depth range 10–35 m) was comparable between hydroacoustics and trawl catches (Fig. 3, $R^2 = 0.40$, $P = 0.009$). The slope (0.69; 95% confidence interval: 0.27–1.35) and intercept (0.73; 95% confidence interval: −0.36–1.40) of the MAR line on $\log_{10}$ transformed values did not differ significantly from the 1:1 fit (slope: $r = -0.30$, $P = 0.26$; intercept: $t = 1.97$, $P = 0.07$), although there was a trend to overestimate fish biomass by the trawl par-

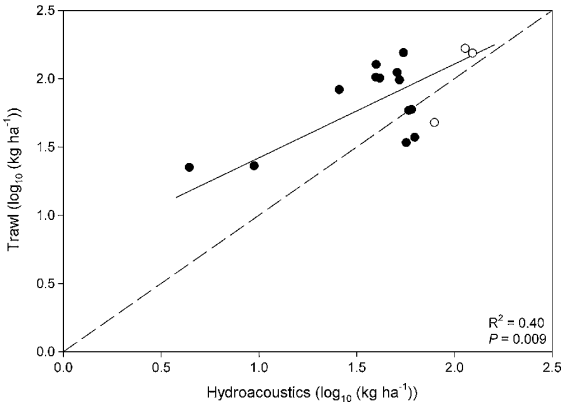

Fig. 3. Scatter plot of $\log_{10}$ transformed total areal fish biomass (kg ha^{-1}) from Lake Stechlin (filled circles) and Lake Breiter Luzin (empty circles) obtained by hydroacoustics or depth-stratified trawl catches. The plot includes the major axis regression line (straight line, with R^2 and P-value given in addition) and 1:1 fit (dashed line).

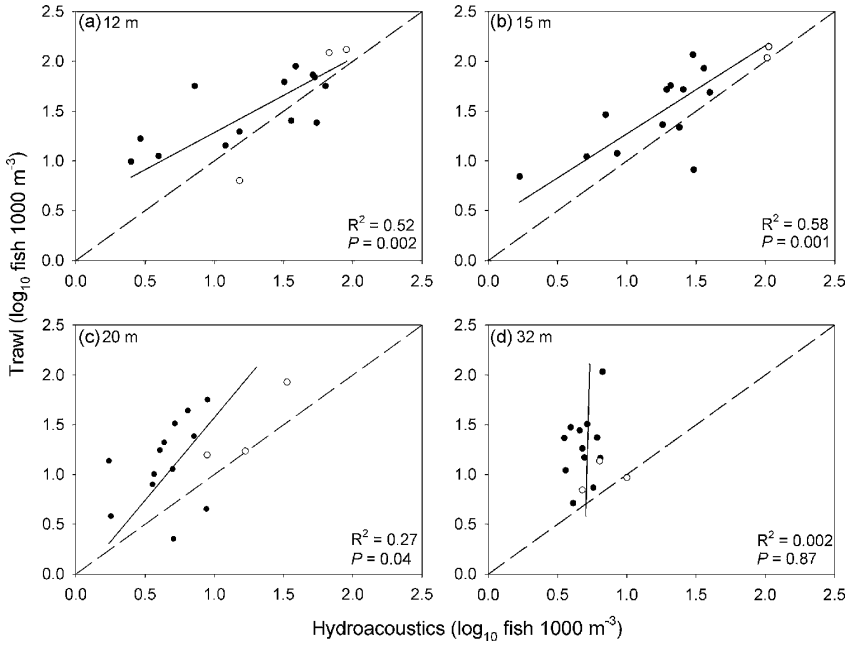

Fig. 4. Scatter plots of depth-specific $\log_{10}$ transformed volumetric fish densities (fish 1000 m^{-3}) from Lake Stechlin (filled circles) and Lake Breiter Luzin (empty circles), obtained by hydroacoustics or trawl catches in 12 m (a), 15 m (b), 20 m (c) and about 32 m (d). All plots include the major axis regression line (straight line, with R^2 and P-value given in addition) and 1:1 fit (dashed line).

Table 1
Statistical details of major axis regressions between $\log_{10}$ transformed volumetric fish densities (fish 1000 m^{-3}) from Lakes Stechlin and Breiter Luzin obtained by hydroacoustics or trawl catches in four different depths. Slopes and intercepts are given with their 95% confidence intervals.

Depth layer (m)	R^2	P-value	Slope	95% CI		Intercept	95% CI	
				Lower	Upper		Lower	Upper
12	0.52	0.002	0.746	0.439	1.054	0.539	0.078	1.000
15	0.58	0.001	0.886	0.516	1.256	0.386	−0.161	0.932
20	0.27	0.04	1.664	−0.364	3.693	−0.091	−1.636	1.453
32	0.02	0.87	52.130	1.567	−4.232	−36.029	4.247	−1.355

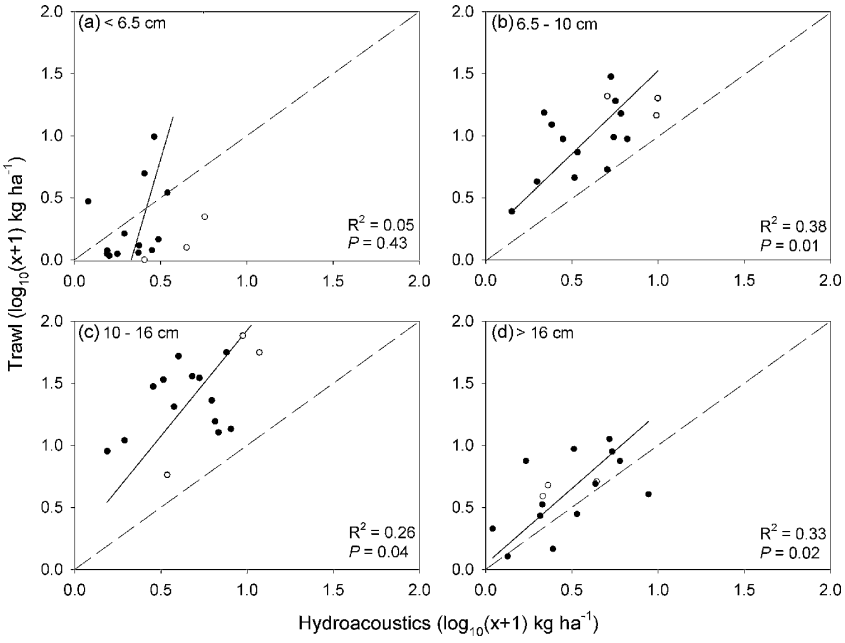

Fig. 5. Scatter plots of size-specific $\log_{10}$ transformed areal fish biomass ($\log_{10}(x+1)$ kg ha^{-1}) from Lake Stechlin (filled circles) and Lake Breiter Luzin (empty circles), obtained by hydroacoustics or trawl catches for fishes <6.5 cm (a), 6.5–10 cm (b), 10–16 cm (c) and >16 cm (d). All plots include the major axis regression line (straight line, with R^2 and P-value given in addition) and 1:1 fit (dashed line).

ticularly at lower fish densities. This was similarly supported from the original (not-transformed) data. On average, the biomass estimates from hydroacoustics were 25% lower in comparison to the trawl catches.

Similarly, depth-specific volumetric abundances estimated by trawling and hydroacoustics were significantly linearly correlated to each other except for the deepest layer operated by the trawl (32 m) (Fig. 4 and Table 1). The slopes of the MAR lines of the upper three layers (12 m, 15 m and 20 m) did not differ significantly from the 1:1 fit (12 m: $r = -0.30$, $P = 0.26$, Fig. 4a; 15 m: $r = -0.14$, $P = 0.61$, Fig. 4b; 20 m: $r = 0.31$, $P = 0.24$, Fig. 4c). Furthermore, the slopes of these three upper trawl depths (Table 1) were not significantly different from each other (Bartlett corrected likelihood ratio (LR) = 2.4, $P = 0.30$), and the common slope estimate was 0.89 (95% confidence interval: 0.613–1.293). In contrast, the slope of the MAR line from the deepest layer (Fig. 3d and Table 1) significantly differed from those of all other regressions (LR = 13.58, $P = 0.004$, pairwise Bonferroni-adjusted comparisons $P \leq 0.001$). The intercepts of the MAR line from the upper three sampling depths likewise did not differ significantly from zero (12 m: $t = 2.0$, $P = 0.06$, Fig. 4a; 15 m: $t = 1.4$, $P = 0.19$, Fig. 4b; 20 m: $t = -0.16$, $P = 0.87$, Fig. 4c). However, the volumetric fish abundances obtained by trawling slightly exceeded those obtained by hydroacoustics in the majority of samplings (Fig. 4).

By splitting the total fish biomass into separate estimates for the four size classes, it became obvious that the estimates for fishes > 6.5 cm TL provided comparable results (Fig. 5 and Table 2). Estimates by hydroacoustics and trawl were significantly linearly correlated, indicated by slopes not differing from one (6.5–10 cm TL: $r = 0.23$, $P = 0.40$, Fig. 5b; 10–16 cm TL: $r = 0.42$, $P = 0.22$, Fig. 5c; >16 cm TL, $r = 0.14$, $P = 0.61$, Fig. 5d). There was no difference between these MAR slopes (LR = 0.35, $P = 0.84$), and the common slope estimate for these three size classes was 1.39 (95% confidence interval: 0.878–2.375). Trawl catches estimated higher biomasses than hydroacoustics for fishes >6.5 cm in most cases (Fig. 5), but the intercepts of MAR did not differ from zero (6.5–10 cm: $t = 0.63$, $P = 0.54$, Fig. 5b; 10–16 cm: $t = 0.42$, $P = 0.68$, Fig. 5c; >16 cm: $t = 0.19$, $P = 0.85$, Fig. 5d). In contrast, there was no correspondence between hydroacoustics and trawl catches for fishes <6.5 cm TL (Fig. 5a, Table 2).

The size-frequency distribution of fishes caught by the trawl and the single echo detections from hydroacoustics differed considerably (Fig. 6, KS-test $Z = 3.00$, $P < 0.001$). However, the mean fish-size was comparable (trawl catches 11.4 cm, hydroacoustics 12.4 cm (−43 dB)). Fishes exceeding 21.5 cm TL were not at all caught by the trawl (Fig. 6), although their occurrence in the pelagic area was indicated by hydroacoustics (2.3% of all SED). Similarly, the frequency

Table 2
Statistical details of major axis regressions between $\log_{10}$ transformed areal fish biomass ($\log_{10}(x+1)$ kg ha^{-1}) from Lakes Stechlin and Breiter Luzin obtained by hydroacoustics or trawl catches for four different fish sizes. Slopes and intercepts are given with their 95% confidence intervals.

Size class (cm)	R^2	P-value	Slope	95% CI		Intercept	95% CI	
				Lower	Upper		Lower	Upper
<6.5	0.05	0.38	4.756	1.040	−2.728	−1.566	1.288	−0.149
6.5–10	0.38	0.01	1.340	0.642	3.459	0.183	−1.127	0.615
10–16	0.26	0.04	1.707	0.700	9.969	0.221	−5.380	0.903
>16	0.33	0.02	1.215	0.509	3.505	0.044	−1.048	0.380

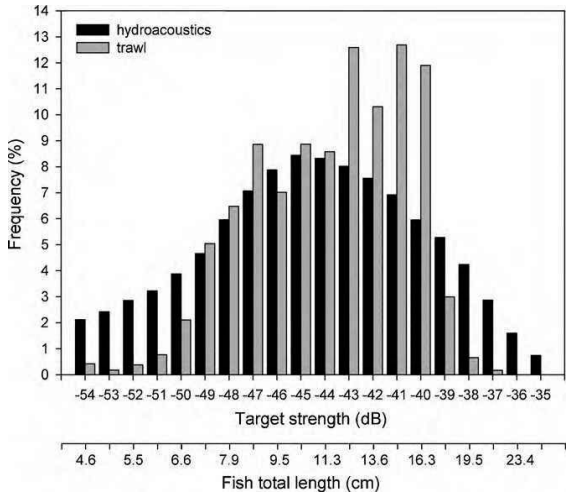

Fig. 6. Target strength (dB)-frequency distributions of hydroacoustic single echo detections and size-frequency (cm) distribution of fishes from the trawl catches. Relationship between target strength and fish total length is based on the conversion formula of Mehner (2006).

of fishes <6.5 cm was higher in hydroacoustic estimates than in the trawl catches.

4. Discussion

Our study shows that estimates of pelagic coregonid densities in two deep lakes by two different methods yielded comparable results. The recorded pelagic fish biomass ranged between 4.4 and 166 kg ha^{-1} depending on lake, sampling gear and season. Nevertheless, we found a significant correlation ($R^2 = 0.40$) between the simultaneously operated trawl catches and the pelagic fish biomass calculated from hydroacoustics. However, in the direct depth-specific comparison, a trend for higher volumetric fish densities obtained by the trawl than by hydroacoustics was detected. With increasing water depth this difference increased. As indicated by differing length–frequency distributions from the echo recordings and trawl catches, medium-sized fishes were slightly more frequent in the trawl catches, whereas frequencies of very small and very large coregonids were underestimated by the trawl, relative to hydroacoustic SEDs.

Our results from these two coregonid-dominated systems indicate that pelagic areal fish biomass can reliably be estimated by either method. The good agreement found here contradicts earlier comparative studies in which a rather poor correspondence between trawl catches and hydroacoustic estimates was found (Jurvelius et al., 2005; Mason et al., 2005; Stockwell et al., 2007). In most of these studies, biomass estimated from trawl catches were substantially lower than those calculated from hydroacoustic surveys. One reason for comparatively high trawl catches in our study may be found in the details of trawl operation. It has recently been demonstrated that many coregonids can escape the trawl during lifting when the vessel stops (Schmidt, 2009). In contrast, our trawling technology allowed lifting the net during the towing runs without completely stopping the boat, thus keeping the speed of net movement constant until the net had reached the water surface. A similarly good correspondence of trawl catches and hydroacoustic fish density estimates has been documented from numerous surveys conducted in Lake Superior (North America) (Yule et al., 2009). These authors predicted pelagic catches as the product from acoustically obtained fish densities with the volume swept by each trawl haul. The predicted fish densities were almost identical to those observed from trawl catches (Yule et al., 2009). This study and our results thus confirm that both methods can give reliable pictures of lake-wide pelagic fish densities in deep lakes, if the technological details of active sampling and hydroacoustic surveys are sufficiently developed.

However, we found lower correspondence between both methods for very small and the largest coregonids, and detected strong discrepancies of density estimates in the deepest layers (>30 m) sampled. We suspect, that the high net speed during lifting, as described above, results in a continued efficient catch of fish even during the upwards movement. This could explain the highly variable catches from deep layers at almost identical hydroacoustic density estimates. Because the coregonids in Lakes Stechlin and Breiter Luzin perform diel vertical migrations and are thus concentrated in the layers just below the thermocline at night (Mehner et al., 2007b; Scharf et al., 2008), the trawl is moved through the layers with highest fish densities during the lifting process from deep layers. This may have caused erroneously high catches, and can be prevented only by applying nets than can be closed already at the sampling depth.

The size selectivity of trawl catches as found in our study has been described elsewhere (e.g. Mous et al., 2002). Our trawl net with mesh sizes in the cod-end of 10 mm knot to knot sampled coregonids efficiently only within a size range of 6.5–17.5 cm. Smaller fishes certainly have escaped from the cod-end, similar to the low efficiency of small-mesh gillnets (<10 mm) to catch coregonids (Mehner and Schulz, 2002). Jurvelius et al. (2005) reported a similar pattern of underestimating abundances of small (<8 cm) smelt (*Osmerus eperlanus* L.) in catches by a trawl with 10 mm mesh size. Generally, however, smaller mesh sizes than 10 mm in the cod-end could not be used because then the maximum achievable trawl speed would have decreased dramatically which in turn leads to a lower catchability of larger fishes (Mous et al., 2002).

The maximum size of coregonids caught by our trawl hauls was 21.5 cm TL, although SEDs with TS equivalent to fishes up to about 30 cm were recorded by hydroacoustics. This lower catch efficiency of the trawl for the largest coregonids may be explained by size-dependent swimming speeds relative to the operation speed of the trawl. Schmidt (2009) found mean swimming speeds of vendace up to 2.4 m s^{-1} in the mouth of a trawl net. Burst speeds of about 2 m s^{-1} can be calculated for 20 cm long fish according to published equations (Wolter and Arlinghaus, 2003). Because absolute swimming speed increases with body length (e.g. Peck et al., 2006), predominantly larger vendace are able to escape capture as mean towing speed was about 1.8 m s^{-1} in our study. A comparable underestimation of larger fish in active gears was found in other trawl surveys targeting vendace (Schmidt, 2009) or multi-species stocks (Kemper and Raat, 1997).

These size-related constraints have to be taken into account also when comparing the overall length–frequency distributions between the SEDs and the trawl catches. Although the mean size calculated from both methods was almost identical, there was a disproportionally higher occurrence of fishes between 12.5 and 16.5 cm in the trawl catches, whereas echoes from very small and very large fishes were more frequent in the hydroacoustic observations. Technological constraints of echo detection may account for some of the deviations. A full correspondence between SED and fish length can be obtained only if the horizontal orientation of fish is always perfectly perpendicular to the acoustical beam (Simmonds and MacLennan, 2005). In all cases where fish are tilted relative to the acoustical beam, their TS will be smaller than predicted by fish length (Čech and Kubečka, 2002; Frouzova et al., 2005). Records from tilted fish are particularly likely when fish have to balance changes in buoyancy during vertical migrations (Eckmann, 1991; Torgersen and Kaartvedt, 2001; Čech and Kubečka, 2002). Therefore, we cannot exclude that the smoothed frequency distribution

of SEDs relative to that of fish caught by the trawl is caused in part by the highly variable TS records obtained from tilted fish. Comparable to our results, Mason et al. (2005) calculated similar mean fish lengths from hydroacoustics and midwater trawling, and the length–frequency distribution derived from hydroacoustic target strengths was smoothed without the single peaks representing certain size classes as found in the trawl catches. Accordingly, length distributions based on acoustic measurements are less precise in comparison to net-based approaches (Godlewska and Świerzowski, 2003).

There are two potential advantages if midwater trawl catches and hydroacoustics can substitute each other in estimating the pelagic fish densities in deep lakes. First, it will only rarely be possible to conduct simultaneous trawl and hydroacoustic surveys over a large range of lakes due to constraints in manpower and finances. At least for pelagic fish assemblages dominated by one species or an assemblage mixture composed of species with similar habitus such as vendace and smelt, large-scale patterns of fish densities can be compared across a variety of deep lakes, even if some density estimates have been obtained by trawl and others by hydroacoustics. Second, either one of the methods may be applied in addition to the standardized fishing by pelagic gillnets required by the EU-WFD. Despite the importance of incorporating information from pelagic habitats in analyses (Diekmann et al., 2005; Lauridsen et al., 2008; Mehner, 2010), data from pelagic gillnet catches should only be used to provide qualitative information on fish stocks (CEN, 2005). The relative abundances (expressed as CPUE data) often do not correlate with the more extensive quantitative data obtained by hydroacoustics (Peltonen et al., 1999) or trawling (Olin and Malinen, 2003). Even in deep, nutrient-poor lakes, pelagic gillnets provided no additional qualitative information (for example with respect to species richness) since the pelagic area is usually dominated by salmonids, that are caught by the benthic nets as well (Diekmann et al., 2005; Deceliere-Vergès and Guillard, 2008). However, the abundance of pelagic salmonids is sensitive to anthropogenic disturbance (Brämick et al., 2008). Coregonids usually decline in response to increasing nutrient levels of lakes (Persson et al., 1991; Eckmann and Rösch, 1998). This decline of coregonid densities over a gradient of lake productivity was only moderately well reflected by a combination of catches from benthic and pelagic gillnets (Garcia et al., 2006; Mehner et al., 2008). Hence, additional sampling with active gears or hydroacoustics in coregonid-dominated lakes seems to be advantageous for understanding the potentially subtle response of lake fish assemblages to anthropogenic stressors (Kubečka et al., 2008).

5. Conclusion

Night-time hydroacoustics and stratified trawl sampling are adequate approaches to monitor pelagic fish densities in coregonid-dominated lakes. Both methods can provide comparable information on areal fish densities in the pelagic zone, if their techniques, applications and data analyses are well developed. Information on pelagic fish densities can be additionally incorporated into the assessment procedure to define the ecological status of deep coregonid-dominated lakes as stipulated by the WFD. In multi-species systems where information on species contributions and detailed size spectra are needed, a combination of hydroacoustics with trawl catches is favoured (cf. Mason et al., 2005).

Acknowledgements

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Appendix A.

Summary of the trawl surveys conducted at Lakes Stechlin and Breiter Luzin.

Lake	Month/year	Trawl depth (m)	Towed distance (m)	Fishes (n)	Mass (g)
Stechlin	March 2005	10–13	817	136	3035
		16–19	817	97	1920
		20–23	680	383	4490
		31–34	840	903	8860
	April 2005	10–13	1283	252	3530
		13–16	817	90	520
		20–23	907	72	330
		31–34	1050	155	1240
	May 2005	10–13	817	91	1680
		13–16	933	65	640
		21–24	620	85	570
		31–34	747	82	530
	June 2005	12–15	933	578	11,550
		13–16	1050	546	9600
		25–28	813	82	700
		30–33	747	222	1780
	July 2005	10–13	933	644	4630
		13–16	817	693	6690
		22–25	800	350	4430
		31–34	800	188	2220
	August 2005	10–13	1050	764	8760
		13–16	1050	511	5660
		23–26	800	36	290
		29–32	–	–	–
	September 2005	11–14	933	830	3860
		14–17	933	1086	6760
		25–28	800	168	2200
		29–32	700	194	2540
	October 2005	11–14	817	116	2540
		13–16	817	424	7020
		24–27	600	105	1820
		29–32	500	91	1050
	November 2005	11–14	817	80	519
		16–19	817	464	9390
		24–27	600	195	2150
		30–33	600	192	1850
	December 2005	11–14	700	394	5420
		13–16	700	203	3560
		24–27	600	145	1520
		31–34	500	116	1000
	June 2006	11–14	933	525	4190
		14–17	700	57	620
		24–27	700	79	730
		30–33	700	102	880
	June 2008	10–13	1200	289	5310
		14–17	1600	346	7420
		27–30	1200	27	250
		32–35	1100	81	1380
	June 2009	11–14	1300	329	5730
		14–17	1050	242	3570
		22–25	500	19	220
		30–33	800	41	390
Breiter Luzin	April 2008	10–13	1633	103	1170
		14–17	–	–	–
		23–26	1300	1099	9270
		30–33	1300	177	2280
	August 2008	10–13	1633	2131	23,840
		14–17	1867	2019	24,050
		23–26	1300	223	4260
		32–35	1300	91	2220

Appendix A (*Continued*)

Lake	Month/year	Trawl depth (m)	Towed distance (m)	Fishes (n)	Mass (g)
	August 2009	10–13	1400	1703	13,360
		14–17	1867	2606	27,670
		24–27	1200	188	2800
		28–31	1000	93	1020
Total				24,398	279,485

References

Adams, J.V., Argyle, R.L., Fleischer, G.W., Curtis, G.L., Stickel, R.G., 2006. Improving the design of acoustic and midwater trawl surveys through stratification, with an application to Lake Michigan prey fishes. North Am. J. Fish. Manage. 26, 612–621.

Anwand, K., Valentin, M., Mehner, T., 2003. Species composition, growth and feeding ecology of fish community in Lake Stechlin – an overview. Arch. Hydrobiol. Spec. Iss. Adv. Limnol. 58, 237–246.

Appelberg, M., Berger, H.M., Hesthagen, T., Kleiven, E., Kurkilahti, M., Raitaniemi, J., Rask, M., 1995. Development and intercalibration of methods in Nordic freshwater fish monitoring. Water Air Soil Pollut. 85, 401–406.

Argyle, R.L., 1992. Acoustics as a tool for the assessment of Great-Lakes forage fishes. Fish. Res. 14, 179–196.

Balk, H., Lindem, T., 2007. Sonar4 and Sonar5-Pro Post Processing Systems. Operator Manual, Version 5.9.7. Balk and Lindem Data Acquisition, Oslo, Norway.

Beier, U., 2001. Habitat distribution and size structure in freshwater fish communities: effects of vendace on interactions between perch and roach. J. Fish Biol. 59, 1437–1454.

Bethke, E., Arrhenius, F., Cardinale, M., Hakansson, N., 1999. Comparison of the selectivity of three pelagic sampling trawls in a hydroacoustic survey. Fish. Res. 44, 15–23.

Brandt, S.B., Mason, D.M., Patrick, E.V., Argyle, R.L., Wells, L., Unger, P.A., Stewart, D.J., 1991. Acoustic measures of the abundance and size of pelagic planktivores in Lake-Michigan. Can. J. Fish. Aquat. Sci. 48, 894–908.

Brämick, U., Diekmann, M., Lemcke, R., Mehner, T., 2008. Assessing shifts in fish assemblages of German large lakes by literature data and commercial catch statistics. Fund. Appl. Limnol. 171, 87–103.

Čech, M., Kubečka, J., 2002. Sinusoidal cycling swimming pattern of reservoir fishes. J. Fish Biol. 61, 456–471.

CEN (European Committee for Standardisation), 2005. Water Quality – Sampling of Fish with Multi-mesh Gill Nets, EN 14757. CEN, Brussels.

Coll, C., de Morais, L.T., Lae, R., Lebourges-Dhaussy, A., Simier, M., Guillard, J., Josse, E., Ecoutin, J.M., Albaret, J.J., Raffray, J., Kantoussan, J., 2007. Use and limits of three methods for assessing fish size spectra and fish abundance in two tropical man-made lakes. Fish. Res. 83, 306–318.

Cowx, I.G., 1996. The integration of fish stock assessment into fisheries management. In: Cowx, I.G. (Ed.), Stock Assessment in Inland Fisheries. Fishing News Books, Blackwell Science, Oxford, pp. 495–506.

Deceliere-Vergès, C., Guillard, J., 2008. Assessment of the pelagic fish populations using CEN multi-mesh gillnets: consequences for the characterization of the fish communities. Knowl. Manage. Aquat. Ecosyst. 389, 04.

Diekmann, M., Brämick, U., Lemcke, R., Mehner, T., 2005. Habitat-specific fishing revealed distinct indicator species in German lowland lake fish communities. J. Appl. Ecol. 42, 901–909.

Doroszczyk, L., Długoszewski, B., Kanigowska, E., Godlewska, M., 2007. Hydroacoustic monitoring of vendace in selected Mazurian lakes. Arch. Pol. Fish. 15, 129–140.

Eckmann, R., 1991. A hydroacoustic study of the pelagic spawning behavior of whitefish (*Coregonus lavaretus*) in Lake Constance. Can. J. Fish. Aquat. Sci. 48, 995–1002.

Eckmann, R., Rösch, R., 1998. Lake Constance fisheries and fish ecology. Arch. Hydrobiol. Spec. Iss. Adv. Limnol. 53, 285–301.

Elliott, J.M., Fletcher, J.M., 2001. A comparison of three methods for assessing the abundance of Arctic charr, *Salvelinus alpinus*, in Windermere (northwest England). Fish. Res. 53, 39–46.

European Union, 2000. Directive 2000/60/EC of the European Parliament and of the council establishment a framework of the community action in the field of water policy. Eur. Comm. Off. J. Eur. Commun. L327, 1.

Frouzova, J., Kubečka, J., Balk, H., Frouz, J., 2005. Target strength of some European fish species and its dependence on fish body parameters. Fish. Res. 75, 86–96.

Garcia, X.F., Diekmann, M., Brämick, U., Lemcke, R., Mehner, T., 2006. Correlations between type-indicator fish species and lake productivity in German lowland lakes. J. Fish Biol. 68, 1144–1157.

Gjelland, K.O., Bohn, T., Horne, J.K., Jensvoll, I., Knudsen, F.R., Amundsen, P.A., 2009. Planktivore vertical migration and shoaling under a subarctic light regime. Can. J. Fish. Aquat. Sci. 66, 525–539.

Godlewska, M., Świerzowski, A., 2003. Hydroacoustical parameters of fish in reservoirs with contrasting levels of eutrophication. Aquat. Living Resour. 16, 167–173.

Guillard, J., Vergès, C., 2007. The repeatability of fish biomass and size distribution estimates obtained by hydroacoustic surveys using various sampling strategies and statistical analyses. Int. Rev. Hydrobiol. 92, 605–617.

Helland, I.P., Freyhof, J., Kasprzak, P., Mehner, T., 2007. Temperature sensitivity of vertical distributions of zooplankton and planktivorous fish in a stratified lake. Oecologia 151, 322–330.

Hoggarth, D.D., Abeyasekera, S., Arthur, R.I., Beddington, J.R., Burn, R.W., Halls, A.S., Kirkwood, G.P., McAllister, M., Medley, P., Mees, C.C., Parkes, G.B., Pilling, G.M., Wakeford, R.C., Welcomme, R.L., 2006. Stock assessment for fishery management – a framework guide to the stock assessment tools of the Fisheries Management Science Programme (FMSP). In: FAO Fish. Tech. Pap. No. 487.

Jurvelius, J., Auvinen, H., Kolari, I., Marjomäki, T.J., 2005. Density and biomass of smelt (*Osmerus eperlanus*) in five Finnish lakes. Fish. Res. 73, 353–361.

Kemper, J.H., Raat, A.J.P., 1997. Hydroacoustic assessment of the fish stock in Theodorushaven, a small Dutch harbour. Fish. Manage. Ecol. 4, 63–71.

Kubečka, J., Hohausová, E., Matěna, J., Peterka, J., Amarasinghe, U.S., Bonar, S.A., Hateley, J., Hickley, P., Suuronen, P., Tereschenko, V., Welcomme, R., Winfield, I.J., 2008. The true picture of a lake or reservoir fish stock: a review of needs and progress. Fish. Res. 96, 1–5.

Lauridsen, T.L., Landkildehus, F., Jeppesen, E., Jørgensen, T.B., Søndergaard, M., 2008. A comparison of methods for calculating catch per unit effort (CPUE) of gill net catches in lakes. Fish. Res. 93, 204–211.

Legendre, P., Legendre, L., 1998. Numerical ecology. Number 20 in Developments in Environmental Modelling, 2nd ed. Elsevier, Amsterdam.

Mason, D.M., Johnson, T.B., Harvey, C.S., Kitchell, J.F., Schram, S.T., Bronte, C.R., Hoff, M.H., Lozano, S.J., Trebitz, A.S., Schreiner, D.R., Lamon, E.C., Hrabik, T., 2005. Hydroacoustic estimates of abundance and spatial distribution of pelagic prey fishes in western Lake Superior. J. Great Lakes Res. 31, 426–438.

Mehner, T., 2010. No empirical evidence for community-wide top-down control of prey fish density and size by fish predators in lakes. Limnol. Oceanogr. 55, 203–213.

Mehner, T., 2006. Prediction of hydroacoustic target strength of vendace (*Coregonus albula*) from concurrent trawl catches. Fish. Res. 79, 162–169.

Mehner, T., Diekmann, M., Gonsiorczyk, T., Kasprzak, P., Koschel, R., Krienitz, L., Rumpf, M., Schulz, M., Wauer, G., 2008. Rapid recovery from eutrophication of a stratified lake by disruption of internal nutrient load. Ecosystems 11, 1142–1156.

Mehner, T., Gassner, H., Schulz, M., Wanzenböck, J., 2003. Comparative fish stock estimates in Lake Stechlin by parallel split-beam echosounding with 120 kHz. Arch. Hydrobiol. Spec. Iss. Adv. Limnol. 58, 227–236.

Mehner, T., Holmgren, K., Lauridsen, T.L., Jeppesen, E., Diekmann, M., 2007a. Lake depth and geographical position modify lake fish assemblages of the European 'Central Plains' ecoregion. Freshw. Biol. 52, 2285–2297.

Mehner, T., Kasprzak, P., Hölker, F., 2007b. Exploring ultimate hypotheses to predict diel vertical migrations in coregonid fish. Can. J. Fish. Aquat. Sci. 64, 874–886.

Mehner, T., Schulz, M., 2002. Monthly variability of hydroacoustic fish stock estimates in a deep lake and its correlation to gillnet catches. J. Fish Biol. 61, 1109–1121.

Milne, S.W., Shuter, B.J., Sprules, W.G., 2005. The schooling and foraging ecology of lake herring (*Coregonus artedi*) in Lake Opeongo, Ontario, Canada. Can. J. Fish. Aquat. Sci. 62, 1210–1218.

Mous, P.J., van Densen, W.L.T., Machiels, M.A.M., 2002. The effect of smaller mesh sizes on catching larger fish with trawls. Fish. Res. 54, 171–179.

Müller, R., 1992. Trophic state and its implications for natural reproduction of Salmonid fish. Hydrobiologia 243, 261–268.

Olin, M., Malinen, T., 2003. Comparison of gillnet and trawl in diurnal fish community sampling. Hydrobiologia 506, 443–449.

Peck, M.A., Buckley, L.J., Bengtson, D.A., 2006. Effects of temperature and body size on the swimming speed of larval and juvenile Atlantic cod (*Gadus morhua*): implications for individual-based modelling. Environ. Biol. Fish. 75, 419–429.

Peltonen, H., Ruuhijävi, J., Malinen, T., Horppila, J., 1999. Estimation of roach (*Rutilus rutilus* (L.)) and smelt (*Osmerus eperlanus* (L.)) stocks with virtual population analysis, hydroacoustics and gillnet CPUE. Fish. Res. 44, 25–36.

Persson, L., Diehl, S., Johansson, L., Andersson, G., Hamrin, S.F., 1991. Shifts in fish communities along the productivity gradient of temperate lakes – patterns and the importance of size-structured interactions. J. Fish Biol. 38, 281–293.

Rask, M., Olin, M., Ruuhijärvi, J., 2010. Fish-based assessment of ecological status of Finnish lakes loaded by diffuse nutrient pollution from agriculture. Fish. Manage. Ecol. 17, 126–133.

R Development Core Team, 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Wien. http://www.R-project.org.

Scharf, J., 2007. *Mysis relicta* (Lovén) in the pelagic food web of Lake Breiter Luzin. Dissertation. Humbolt University, Berlin (in German).

Scharf, J., Krappe, M., Koschel, R., Waterstraat, A., 2008. Feeding of European cisco (*Coregonus albula* and *C-lucinensis*) on the glacial relict crustacean *Mysis relicta* in Lake Breiter Luzin (Germany). Limnologica 38, 147–158.

Schmidt, M.B., 2009. Reactions of vendace (*Coregonus albula*, Linnaeus 1758) towards an approaching pelagic pair-trawl observed by split-beam echosounding. Fish. Res. 96, 95–101.

Schmidt, M.B., Gassner, H., Meyer, E., 2005. Distribution and biomass of an underfished vendace, *Coregonus albula*, population in a mesotrophic German reservoir. Fish. Manage. Ecol. 12, 169–175.

Simmonds, E.J., MacLennan, D.N., 2005. Fisheries Acoustics: Theory and Practice. Fish and Fisheries Series, 2nd ed. Blackwell, Oxford, UK.

Stockwell, J.D., Yule, D.L., Hrabik, T.R., Adams, J.V., Gorman, O.T., Holbrook, B.V., 2007. Vertical distribution of fish biomass in Lake Superior: implications for day bottom trawl surveys. North Am. J. Fish. Manage. 27, 735–749.

Świerzowski, A., 2001. Diel variations in the vertical distribution and density of vendace *Coregonus albula* (L.) in Pluszne Lake. Arch. Pol. Fish. 9, 147–156.

Torgersen, T., Kaartvedt, S., 2001. In situ swimming behaviour of individual mesopelagic fish studied by split-beam echo target tracking. ICES J. Mar. Sci. 58, 346–354.
Warton, D.I., Wright, I.J., Falster, D.S., Westoby, M., 2006. Bivariate line-fitting methods for allometry. Biol. Rev. 81, 259–291.
Waterstraat, A., Krappe, M., Rumpf, M., Riel, P., Koschel, R., Casper, P., Ginzel, G., Gonsiorczyk, T., Kasprzak, P., Krienitz, L., Mehner, T., Scharf, J., Schulz, M., Thomas, M., Kotusz, J., Kusnierz, J., Witkowski, A., 2003. Voruntersuchungen zum Erprobungs-und Entwicklungsvorhaben, Schutz der gefährdeten glazialen Reliktfauna der nährstoffarmen Feldberger Seen durch einen ganzheitlichen Gewässerschutz. Report for the Federal Agency for Nature Conservation, Germany (in German).
Wolter, C., Arlinghaus, R., 2003. Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance. Rev. Fish Biol. Fish. 13, 63–89.
Yule, D.L., Stockwell, J.D., Schreiner, D.R., Evrard, L.M., Balge, M., Hrabik, T.R., 2009. Can pelagic forage fish and spawning cisco (*Coregonus artedi*) biomass in the western arm of Lake Superior be assessed with a single summer survey? Fish. Res. 96, 39–50.

Paper IV

Emmrich, **M.**, Brucet, S., Ritterbusch, D., and Mehner, T.

Size spectra of lake fish assemblages: responses along gradients of general environmental factors and intensity of lake-use.

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Size spectra of lake fish assemblages: responses along gradients of general environmental factors and intensity of lake-use

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SUMMARY

1. The size structure of communities is shaped by biotic and abiotic interactions. Therefore, comparative analyses of size spectra may reveal the major drivers governing patterns and processes in size-structured communities.
2. We tested the suitability of non-taxonomic, size-related variables as tools for elucidating systematic shifts in lake fish assemblages along the gradients of environmental factors and lake-use intensity. Catch data of multimesh gillnets from 78 lowland lakes in northern Germany were analysed.
3. We first identified the correlations, and hence inherent redundancy, among 18 size-related variables. The correspondence between eight weakly correlated size variables and descriptors of lake morphometry, lake productivity, lake-use intensity and taxonomic and functional fish-assemblage composition was tested using ordination by non-metric multidimensional scaling (NMDS). The three axes of the NMDS analysis were strongly correlated with five size variables, which in turn corresponded to lake area, mean and maximum depth, total phosphorus and chlorophyll *a* concentration, predator abundance and predator/prey length ratios (PPLR).
4. The number of size classes increased with increasing lake area. The slopes of normalised length spectra were flatter (less negative) and size diversity was higher in deep, less nutrient-rich lakes and in lakes with a higher numerical predator abundance, indicating a higher relative abundance of large fish. The exponent of the Pareto type II mass spectra was larger and maximum fish length was smaller in shallow, nutrient-rich lakes and in lakes with lower predator biomass and smaller PPLR, indicating a higher relative proportion of medium-sized fish.
5. Analyses of size spectra at regional scales can contribute important information to the evaluation of the ecological quality of lakes. We suggest further studies at a broader range of environmental and geographical scales to understand the subtle response of size-related variables to biotic interactions, abiotic stressors and geographical patterns.

Keywords: body size, lake morphometry, multilake analyses, multimesh gillnets, size diversity

Introduction

Size is a key property of organisms affecting almost all aspects of their life history and ecology, such as respiration, ingestion, reproduction and life span

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(Peters, 1983; Calder, 1984). Owing to fast growth during ontogeny and substantial size differences between ontogenetic stages, many populations, including fish, are strongly size structured (Werner & Gilliam, 1984; Post, Parkinson & Johnston, 1999; Blanchard *et al*., 2009). However, the size structure of populations can be further shaped by biotic interactions, such as predation and competition, and by factors including productivity or physical attributes of the habitats (Persson *et al*., 1991; Wellborn, Skelly & Werner, 1996). Accordingly, size-based analyses can be useful in describing communities and can help to identify the complex effects of biotic and abiotic influences (Strayer, 1991; De Leeuw *et al*., 2003; Brucet *et al*., 2010).

Pioneered by Sheldon, Prakash & Sutcliffe (1972), analyses of size distributions have been applied to various fields of aquatic research, primarily targeting plankton (e.g. Sprules & Munawar, 1986; Gamble *et al*., 2006). Furthermore, impacts of fisheries on marine fish stocks have been documented by size-spectra analyses (e.g. Rochet & Trenkel, 2003; Sweeting *et al*., 2009). Petchey & Belgrano (2010) suggested that similar systematic changes in size spectra, as observed for exploited marine fish stocks, occur in other systems under different types of environmental pressures. Indeed, although size-based approaches have been less frequently applied to freshwater fish assemblages, the few existing studies suggest that size structures can adequately characterise systematic shifts between lake fish assemblages along the gradients of water quality (Holmgren & Appelberg, 2000; De Leeuw *et al*., 2003).

Assemblages of lake fish in Europe are characterised by low regional species richness and low species variability between lakes and are in general dominated by only a few generalist species that are widespread along nutrient gradients (Tonn *et al*., 1990; Tammi *et al*., 2003). Recent analyses of lakes within the European Central Plain ecoregion have revealed that only a low amount of taxonomic variability (species diversity and relative species abundance) was related to morphometric, human-use intensity and geographical variables (Mehner *et al*., 2005, 2007). Furthermore, the originally well-established conceptual model describing a gradual succession of lake fish assemblages from a numerical dominance by Salmoniformes to a dominance of perch (*Perca fluviatilis* L.) and finally cyprinids along an increasing nutrient gradient in Europe has recently been challenged by contrary evidence from fish assemblages in Germany (Diekmann *et al*., 2005; Mehner *et al*., 2005), Sweden (Holmgren & Appelberg, 2000) and Finland (Olin *et al*., 2002). Accordingly, the taxonomic composition of fish assemblages has been shown to be insensitive to the ecological status of lakes in Europe. Therefore, we investigated whether non-taxonomic analyses of size structure can detect shifts in the structure of fish assemblages along gradients in German temperate lakes characterised by a depauperate regional fish-species pool.

Several empirical studies have shown substantial differences in the size structure of fish assemblages in lakes, with a shift towards smaller individuals in more eutrophic systems (Jeppesen *et al*., 2000; Godlewska & Świerzowski, 2003) and with a higher proportion of large fish in large and deep systems (Holmgren & Appelberg, 2000; Beier, 2001; Wilde & Pope, 2004; Arend & Bain, 2008). In addition to morphometric and chemical characteristics of lakes, the taxonomic and functional differences between lake fish assemblages can also modify their size structures. Persson *et al.* (1991) and Mehner (2010) demonstrated that the size of prey available was positively coupled with the proportion and size of predators in assemblages. Additionally, stunted growth, the plastic response of fish to unfavourable environmental conditions and predominantly observed in discrete systems such as lakes (Roff, 1992), is known for many freshwater fish families including species most frequently occurring in European lakes (see Ylikarjula, Heino & Dieckmann, 1999 and references therein). These empirical observations indicate that both abiotic and biotic factors shape the size structure of fish assemblages. However, a comprehensive comparison of size-related variables of fish assemblages in response to both biotic and abiotic gradients is still missing (Jennings *et al*., 2001; Griffiths, 2006).

The aim of our study was to test the applicability of non-taxonomic, size-related variables as a tool to elucidate systematic shifts in lake fish assemblages along environmental and lake-use intensity gradients by analysing catch data from standardised surveys by multimesh gillnets. In particular, we combined several size-related variables, originally derived from plankton and marine fisheries research, to compare (i) their consistency and variability when applied to

multimesh gillnet catches of fish in lakes, (ii) their intercorrelations and hence inherent redundancy and (iii) their correspondence with descriptors of lake morphometry and productivity, lake-use intensity and taxonomic and functional classifications of fish assemblages.

Methods

Fish sampling

The data set comprised 78 lakes, including the 65 lakes analysed by Mehner *et al.* (2005). The lakes are located in the north German lowlands, ecoregion 'Central Plains' (Illies, 1978). The fish assemblages were sampled according to the European standard for gillnet surveys EN 14757 (CEN (European Committee for Standardisation), 2005) between 2001 and 2009. The sampling procedure for 55 of the lakes differed slightly from the standard protocol, because for those lakes, the sampling effort was split with the first half of the nets set during late summer or early autumn and the second half set during the subsequent spring (cf. Mehner *et al.*, 2005). Each lake was divided into depth strata according the European standard, and each stratum was randomly sampled by a pre-defined number of benthic gillnets (type NORDEN: length 30 m; height 1.5 m; 12 panels of 2.5 m each with mesh sizes (knot to knot) of 5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm), depending on lake area and maximum depth (Appelberg, 2000; CEN, 2005). Deep lakes (maximum depth >6 m) were additionally sampled with a row of pelagic nets [similar type as the benthic ones, but of 3 m height and 27.5 m length (5 mm mesh panel missing)] placed over the deepest location in each lake. In the case of complete repeated surveys in the same lake over several years, only data from the most recent sampling campaign were included. Fish were measured (total length, TL) to the nearest cm and weighed (fresh mass, FM) to the nearest gram. Total unweighted catches from both benthic and pelagic habitats were incorporated in the analyses, independently of the relative contribution of benthic and pelagic catches to the total.

Ideally, analyses of catch data should be restricted to size classes for which the catch efficiency of the gear is maximised (Jennings & Dulvy, 2005) and consistent (Rochet & Trenkel, 2003). As young-of-the-year fish are usually underestimated in multimesh gillnet catches (Olin & Malinen, 2003; Olin, Malinen & Ruuhijärvi, 2009; Prchalová *et al.*, 2009), we excluded all individuals <8 cm TL from the analyses. No correction was applied to large fish. Catch efficiency of multimesh gillnets for large size classes has not yet been investigated in detail but is assumed to result in only slight overestimates (Prchalová *et al.*, 2009), as catchability does not change strongly with increasing size (Kurkilahti & Rask, 1996). The widely applied standardised norm EN 14757 (CEN, 2005) for sampling lake fish assemblages provides a reliable basis for comparing the size distribution of fish assemblages. Single sample occasions provide an unbiased picture of the size structure of lake fish assemblages (Holmgren, 1999; Holmgren & Appelberg, 2000) and the relative size structure of the gillnet catches did not suffer from the saturation effect, which can underestimate relative fish abundance (Olin *et al.*, 2004; Prchalová *et al.*, 2011).

Size-related variables

In total, 18 size-related variables derived from 14 size-based approaches (listed below) were calculated from the gillnet catches (Table 1). For the calculation of linearised size spectra, gillnet catches were standardised by calculating the average number of fish per net within each size class (catch per unit effort, CPUE). The pelagic nets (3 m in height and approximately double the area of benthic ones) were considered as two nets for the calculation of CPUE. For all other size-related variables, no catch standardisation was necessary, because the size-related variables and the number of nets or the number of fish caught were only weakly correlated (Spearman's $r < |0.28|$, resp. $r_s < |0.43|$).

(1) The geometric mean fish length [L_{gmean} (cm)] and (2) variance (L_{var}) (based on length data) were calculated for the entire catch. We further compared (3) the skewness (L_{skew}) and (4) kurtosis (L_{kurt}) of the length–frequency distributions (LFD) (1-cm class intervals). We selected the 99.9th percentile (fish-length data from all lakes pooled) as the upper length limit (50 cm) to reduce the number of zeros in the LFD. Frequencies were $\log_{10}(x + 1)$-transformed. (5) The number of size classes (n SC) with at least one individual (1-cm intervals) was counted, and (6) the interquartile range [IQR (cm)] (the difference between the third and first quartiles), i.e. the size range including 50% of all individuals from the catch, was

Table 1 Characteristics and variability of 18 size-related variables from fish assemblages sampled in 78 German lowland lakes including variable range, mean, median and coefficient of variation (CV). For a detailed description of the variables, see Methods

Size-related variables (Unit)	Code	Range		Mean	Median	CV (%)
		Lower	Upper			
Geometric mean length (cm)	L_{gmean}	9.91	16.65	12.26	12.11	10.21
Variance length data	L_{var}	8.63	123.43	30.29	28.30	51.03
Skewness LFD	L_{skew}	−0.40	1.48	0.49	0.44	71.96
Kurtosis LFD	L_{kurt}	−1.73	0.82	−0.92	−1.04	57.41
Number of size classes	*n* SC	20.00	44.00	31.56	32.00	16.83
Interquartile range length data (cm)	IQR	2.00	13.00	5.71	6.00	35.41
Maximum length (cm)	L_{max}	32.00	105.00	58.01	55.00	27.93
95% percentile	L_{95}	14.00	30.00	22.69	23.00	15.74
Proportion quality length (%)	L_{qual}	0.07	6.96	1.46	1.18	89.57
Fulton's condition factor assemblage	K_a	0.79	1.32	1.06	1.05	9.93
Size diversity	SD (μ)	1.07	2.25	1.80	1.86	14.14
Slope normalised length spectra	S NLS	−1.46	−0.24	−0.90	−0.90	3.19
R^2 normalised length spectra	R^2 NLS	0.61	0.95	0.80	0.80	10.88
Slope normalised mass spectra	S NMS	−0.75	−0.19	−0.51	−0.51	4.48
R^2 normalised mass spectra	R^2 NMS	0.41	0.98	0.86	0.90	7.61
c Pareto type II mass spectra	*c* Par	0.68	8.20	1.96	1.78	45.23
D Pareto type II mass spectra	*D* Par	0.09	107.15	13.39	8.37	116.06
R^2 Pareto type II mass spectra	R^2 Par	0.87	0.99	0.97	0.98	2.51

LFD, length–frequency distribution.

calculated. Then, (7) the maximum length [L_{max} (cm)] was selected from the largest individual caught in the gillnets in each lake, and (8) we selected the 95th percentile of the LFD [L_{95} (cm)] as a size variable. Next, (9) the proportion of fish above 'quality length' [L_{qual} (%)] included the proportion of fish exceeding the minimum size limit for anglers. We used the median minimum size limit of the five German federal states in which the 78 lakes had been sampled. For species with no minimum size limit, the quality-length threshold was set to 30 cm TL.

Fulton's condition factor (10) was calculated for each fish separately (K_i) by:

$$K_i = \frac{W}{L^3} \cdot 100. \quad (1)$$

The condition factor of the total fish assemblage (K_a) was calculated as the arithmetic mean of K_i:

$$K_a = \frac{\sum_{i=1}^{n} K_i}{n}. \quad (2)$$

Furthermore, (11) size diversity (SD; μ) was calculated for each lake following the nonparametric approach of Quintana *et al.* (2008), which is related to the Shannon diversity index but adapted for continuous variables (herein fish total length) corresponding to the integral form:

$$\mu = -\int_0^{+\infty} p_x(x) \log_2 p_x(x) \mathrm{d}x, \quad (3)$$

where $p_x(x)$ is the probabilty density function of the length of each individual fish.

$P_x(x)$ was calculated using nonparametric kernel estimation by:

$$\hat{\mu}_{\mathrm{kerMC}}(X) = \bar{y} - \frac{1}{n}\sum_{k=1}^{n} \log_2 \left[\frac{1}{n\sqrt{2\pi}\sigma} \sum_{j=1}^{n} \exp\left(-\frac{1}{2} \frac{(yk - yj)^2}{\sigma^2} \right) \right]. \quad (4)$$

Length data were standardised beforehand by division by the sample geometric mean value (Quintana *et al.*, 2008).

We also calculated (12) normalised length spectra (NLS), according to Sprules & Munawar (1986), that were modified to fish-length data. We used $\log_2/2$ size classes to ensure a sufficiently high number of size classes (n = 7 covering a length range of 8–91 cm). All fish >91 cm TL (n = 5) were allocated to the largest class (64–91 cm). The fish in each class were divided by the number of nets and by the width of the size

class and were subsequently $\log_2(x + 1)$-transformed. The transformed abundances were plotted against the $\log_2$ midpoints of each size class, and the slope and coefficient of determination (R^2) of the linear regression lines were compared among the lakes.

Normalised mass spectra (NMS) (13) were analysed similarly to NLS but were modified for fish-mass data (cf. Blanchard *et al.*, 2005; Sweeting *et al.*, 2009). All fish were allocated to $\log_2$ FM classes from 1 (8 g) to 10 (>2048 g). Class 1 summed fish from $\log_2 = 2$ (4 g) and $\log_2 = 3$ (8 g), because individuals with FM <4 g were extremely rare (0.008%) because of the removal of all fish <8 cm TL from the data set. Fish masses within each size class were divided by the number of nets and the span of the size class, subsequently $\log_2(x + 1)$-transformed and finally regressed analogously to the NLS. The slopes and R^2 of the linear regression lines were calculated. Slopes of normalised size spectra (NLS and NMS here) quantify the relative abundance of small and large fish in a sample (Shin & Cury, 2004). A steepening of the slope can be the result of a decreasing number of large fish, an increasing number of small fish or both (Pope & Knights, 1982; Bianchi *et al.*, 2000). For size–abundance relationships, R^2 can be used as a measure of disturbance (i.e. the relative distance from steady state) in a given system (Sprules, Casselman & Shuter, 1983; Choi, Mazumder & Hansell, 1999).

Fish mass spectra (14) were analysed using underlying Pareto type II probability density functions $p_i(FW)$, following the equation

$$p_i(FM) = c(K + D)^c(FM_t + D)^{-(c+1)}, \quad (5)$$

with the cumulative distribution of probability defined as:

$$prob(FM \geq FM_t) = (K + D)^c(FM_t + D)^{-c}, \quad (6)$$

where D is an additive constant, FM is the fresh mass of the individual fish and FM_t is a threshold size (Vidondo *et al.*, 1997). In other words, the term $prob(FM \geq FM_t)$ is calculated for each fish mass as the proportion of all fish larger than or equal to itself:

$$prob(FM \geq FM_t) = \frac{N_{FM \geq FM_t}}{N_t}. \quad (7)$$

The parameters c and D were calculated by regressing $\log(prob(FM \geq FM_t))$ on FM using the iterative nonlinear algorithm $\log(prob(FM \geq FM_t)) = c \log(K + D) - c \log(FM_t + D)$ (Vidondo *et al.*, 1997). Beforehand, fish masses were standardised ($K = 1$) following Winiwarter & Cempel (1992):

$$FM' = \frac{FM}{FM_{\min}}, \quad (8)$$

where the standardised masses (FM') were obtained by dividing the fish masses within a sample (FM) by the minimum mass observed in that sample ($FM_{\min}$).

Finally, we derived three parameters (the exponent c, the additive constant D and R^2) from the nonlinear ordinary least square regressions. Although the ecological meaning of c and D is somewhat difficult to interpret (Quintana *et al.*, 2008) and the response of the parameters to gradients is not yet completely understood (Gamble *et al.*, 2006), they can be used to compare systems (Vidondo *et al.*, 1997). Higher values of c (and D) are obtained in cases of more pronounced curvature in the Pareto type II distribution, whereas lower values represent more linear models. A more linear relationship indicates a higher relative abundance of smaller size classes, while a stronger curvature of the nonlinear regression line indicates a more equal distribution of the sizes with a higher relative abundance of larger size classes (Brucet *et al.*, 2005).

In general, we favoured length-related variables over mass-related ones, as fish mass is often incompletely recorded during field campaigns. In the case of the Pareto type II approach, however, FM data are required (Gamble *et al.*, 2006), as length data result in strong inaccuracies in the parameter estimates (large confidence intervals) owing to the smaller amplitude of fish length compared with FM (M. Emmrich, unpublished). To exclude strongly correlated variables from subsequent analyses, we calculated correlations between all size-related variables and selected only those with Spearman's rank correlation coefficients $r_s < |0.6|$ (see Table 2 for detailed r_s and P-values). In the case of strongly correlated variables, we favoured those for which the loss of original information in the size data was lowest.

Lake variables

Non-metric multidimensional scaling (NMDS) analysis (Kruskal, 1964) was used to analyse size-related fish-assemblage differences. NMDS analysis maximises rank-order correlation between original distance measures and the distances in ordination space. The points (lakes) are moved to minimise stress, which is a

Table 2 Correlation matrix of the 18 size-related variables. The white matrix contains Spearman's r values; the grey matrix contains the corresponding P-values. Weakly correlated variables ($r_s < |0.60|$) that were exposed to the non-metric multidimensional scaling ordination are indicated in boldface. For the full names of the size-related variables, see Table 1

Variables	L_{gmean}	L_{var}	L_{skew}	L_{kurt}	n SC	IQR	L_{max}	L_{95}	L_{qual}	K_a	SD (μ)	S NLS	R^2 NLS	S NMS	R^2 NMS	c Par	D Par	R^2 Par
L_{gmean}	–	0.564	−0.579	−0.590	0.311	0.733	0.157	0.559	0.560	0.197	0.688	0.246	0.655	0.415	−0.403	0.322	0.552	0.078
L_{var}	<0.001	–	−0.696	−0.369	0.673	0.668	0.359	0.853	0.821	0.081	0.825	0.289	0.418	0.460	0.060	0.027	0.442	−0.124
L_{skew}	<0.001	<0.001	–	0.718	−0.567	−0.708	−0.137	−0.812	−0.629	−0.234	−0.751	−0.053	−0.674	−0.184	−0.064	−0.469	−0.787	0.086
L_{kurt}	<0.001	0.001	<0.001	–	−0.184	−0.642	−0.183	−0.421	−0.214	−0.193	−0.655	−0.218	−0.719	−0.231	0.102	−0.472	−0.616	−0.174
n SC	0.006	<0.001	<0.001	0.106	–	0.370	0.387	0.579	0.680	−0.028	0.510	−0.123	0.355	0.007	0.345	−0.145	0.236	0.049
IQR	<0.001	<0.001	<0.001	<0.001	0.001	–	0.208	0.601	0.564	0.233	0.820	0.233	0.631	0.375	−0.188	0.408	0.656	0.026
L_{max}	0.170	0.001	0.233	0.108	<0.001	0.068	–	0.097	0.172	−0.228	0.261	0.203	0.002	0.232	0.049	−0.362	−0.180	0.224
L_{95}	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.399	–	0.806	0.188	0.764	0.195	0.471	0.364	0.093	0.233	0.593	−0.266
L_{qual}	<0.001	<0.001	<0.001	0.060	<0.001	<0.001	0.133	<0.001	–	0.047	0.707	0.243	0.419	0.420	0.059	−0.044	0.378	−0.149
K_a	0.084	0.479	0.040	0.090	0.804	0.040	0.045	0.099	0.680	–	0.152	−0.265	0.280	−0.117	−0.437	0.545	0.436	−0.088
SD (μ)	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.021	<0.001	<0.001	0.185	–	0.296	0.546	0.444	−0.003	0.188	0.530	0.082
S NLS	0.030	0.010	0.646	0.056	0.285	0.040	0.074	0.088	0.032	0.019	0.009	–	0.178	0.914	−0.007	−0.184	−0.034	0.004
R^2 NLS	<0.001	<0.001	<0.001	<0.001	0.001	<0.001	0.989	<0.001	<0.001	0.013	<0.001	0.102	–	−0.067	−0.150	0.481	0.656	0.178
S NMS	<0.001	<0.001	0.108	0.042	0.949	0.001	0.041	0.001	<0.001	0.306	<0.001	<0.001	0.561	–	−0.167	−0.108	0.099	−0.054
R^2 NMS	<0.001	0.600	0.578	0.372	0.002	0.099	0.668	0.419	0.608	<0.001	0.981	0.953	0.190	0.143	–	−0.328	−0.209	−0.025
c Par	0.004	0.818	<0.001	<0.001	0.205	<0.001	0.001	0.040	0.702	<0.001	0.099	0.107	<0.001	0.346	0.003	–	0.830	−0.086
D Par	<0.001	<0.001	<0.001	<0.001	0.038	<0.001	0.114	<0.001	0.001	<0.001	<0.001	0.768	<0.001	0.389	0.067	<0.001	–	−0.157
R^2 Par	0.499	0.280	0.451	0.127	0.669	0.823	0.049	0.019	0.193	0.446	0.474	0.972	0.119	0.641	0.828	0.455	0.170	–

measure of mismatch between both distances. Three matrices were constructed. The main matrix contained the eight weakly correlated size-related variables that were normalised by their maxima. Initially, the NMDS analysis was performed by selecting random start configuration, six dimensions, Euclidean distance and 200 iterations. Monte Carlo simulation (50 runs with real and randomised data) was included to check whether a similar final stress value was obtained by chance. The optimum dimensionality was derived from the scree plot of stress versus dimensionality. The configuration of the optimal dimensionality was selected as the new starting configuration for the final run without a further change in dimensionality. Additionally, Spearman's correlations of size-related variables with the significant axes were calculated.

In two comatrices, a total of 17 abiotic and biotic descriptors of the 78 lakes and their fish assemblages were summarised. The first comatrix included nine abiotic variables, divided into (1) variables describing lake morphometry (n = 5 variables), (2) lake productivity variables (n = 2) and (3) variables characterising lake-use intensity (n = 2). In detail, the morphometric variables (1) consisted of (variable range in brackets) lake area (50–11 300 ha), maximum depth (1.0–72.3 m), mean depth (0.65–28.6 m), shore length (3.0–123.7 km) and catchment area (190–750 000 ha). The productivity variables (2) encompassed total phosphorus concentration (13.0–330.0 μg L^{-1}) and chlorophyll *a* concentration (Chl *a*) (1.5–287.7 μg L^{-1}), both based on arithmetic averages from samplings taken during the growing season between May and September. Morphometry and productivity variables were $\log_{10}$- or $\log_{10}(x + 1)$-transformed to ensure a linear relationship and to stabilise their variances.

Lake-use intensity (3) (human-use variables, anthropogenic shoreline modifications and fishing activity) was initially assessed on a ranked scale (all variables except fishing activity): category 1 = no impact; category 2 = minor; category 3 = moderate; category 4 = heavy impact. The human-use variables included the frequency of commercial ship passages, the number of recreational boats with and without engines, bathing and fishing activities. Anthropogenic shoreline modifications included bathing places, footbridges/marinas, sheet piles, woody erosion control structures (fascines) and rip-rap habitats. Fishing activity was classified as 1 = no fisheries; 2 = recreational fisheries; 3 = commercial fisheries; 4 = both recreational and commercial fisheries. For the conversion of categorical variables into continuous synthetic ones, we used multiple correspondence analysis (MCA; Tenenhaus & Young, 1985; Greenacre & Blasius, 2006) by building an indicator matrix with a binary coding of the 10 lake-use variables with the four categories of each factor. The principal coordinates for each lake of the first two MCA axes were considered as synthetic lake-use variables (axis 1 + 2 lake use).

To a second comatrix, we added eight biotic variables (4) that describe the taxonomic or functional composition of the fish assemblages in lakes. Three variables reflected taxonomic composition, namely number of species, proportion of cyprinids and proportion of percids (Table 3). Three further variables reflected the predator–prey relationships in the lakes. According to Mehner (2010), pike (*Esox lucius* L.), zander [*Sander lucioperca* (L.)], burbot (*Lota lota* L.), asp [*Aspius aspius* (L.)] and European catfish (*Silurus glanis* L.) were classified as predators (obligatory piscivores). Perch were divided into predatory (TL ≥ 15 cm) and non-predatory (TL < 15 cm) fish (cf. Persson *et al.*, 1992). All other fish were considered as potential prey. We calculated the numerical proportion (%) and biomass proportion (%) of predators in each lake. Predator/prey length ratio (PPLR) was calculated as the ratio between mean predator length and mean prey length.

Finally, two further variables indicated species diversity in the lakes. In correspondence to the size diversity index mentioned earlier (Quintana *et al.*, 2008), we calculated the taxonomic Shannon index (H') by

$$H' = -\sum_{i=1}^{n} p_i \log_2 p_i \tag{9}$$

and evenness (J) as

$$J = \frac{H'}{\log_2 s}, \tag{10}$$

with s representing the number of species.

Taxonomic and functional variables of the fish assemblages were normalised to their maxima, and proportion data were arc-sine square-root-transformed (Sokal & Rohlf, 1995). After ordination of the main matrix (size-related variables) by NMDS analysis, Spearman's rank correlations between the lake's scores per dominant axis and the lake-specific variables

Table 3 Spearman's rank correlation coefficients between variables of lake morphometry, lake productivity, lake-use intensity and taxonomic and functional descriptors of fish assemblages and the lake scores of the three dominant axes (predicted variance in brackets) obtained from the non-metric multidimensional scaling (NMDS) analysis. NMDS analysis based on eight size-related variables derived from fish assemblages sampled in 78 lowland lakes in northern Germany. Significantly correlated variables ($r_s > |0.30|$, $P \leq 0.004$) are indicated in boldface

Variables	Unit	Axis 1 (15.6%)	Axis 2 (40.8%)	Axis 3 (40.4%)
Lake morphometry				
Area	ha	**−0.324**	−0.060	−0.090
Shore length	km	−0.214	−0.209	0.045
Maximum depth	m	0.250	**−0.582**	**0.465**
Mean depth	m	**0.319**	**−0.515**	**0.417**
Catchment area	ha	**−0.410**	0.163	−0.165
Lake productivity				
Total phosphorus	μg L^{-1}	−0.275	**0.349**	**−0.472**
Chlorophyll *a*	μg L^{-1}	−0.253	**0.442**	**−0.474**
Lake-use intensity (MCA scores)				
Axis 1 lake use		0.283	−0.010	0.103
Axis 2 lake use		−0.103	0.101	−0.183
Fish assemblage descriptors				
Proportion cyprinids	%	−0.130	0.297	−0.143
Proportion percids	%	0.031	−0.165	−0.021
Proportion predators (biomass)	%	0.125	−0.295	**0.357**
Proportion predators (abundance)	%	0.042	**−0.358**	0.006
Predator/prey length ratio		0.173	0.070	**0.418**
Number of species		**−0.401**	−0.138	0.298
Shannon diversity		−0.167	−0.048	−0.092
Shannon evenness		0.050	0.003	−0.230

included in the two comatrices were calculated. NMDS analysis was performed by PC-Ord for Windows, version 4 (McCune & Mefford, 1999; MJM Software Design, Gleneden Beach, OR, U.S.A.). MCA was computed in R (version 2.7.0; R Development Core Team, 2008) using the ca package (version 0.2.1, 2007; Nenadić & Greenacre, 2007)

Results

Size-related variables

In total, size data of 132,665 fish ≥8 cm total length caught by multimesh gillnets in 78 north German lowland lakes were included in this study. Catch size ranged from 407 to 4248 individuals per lake (mean 1645 individuals).

Differences in range and coefficient of variation (CV) were substantial between the 18 size-related variables tested (Table 1). The highest variability was found in the additive constant D of the Pareto type II mass spectra, the skewness of the length–frequency distributions and in the proportion of fish above quality length. Variability in the slopes and R^2 of the normalised size spectra was similar with lower variability in the slopes in comparison with their corresponding R^2 values.

High values of size diversity were obtained in cases of equally distributed fish lengths (Fig. 1a) or if the catch consists of many different fish lengths (Fig. 1b). For fish-mass data, the relative proportion of small- and medium-sized fish has the strongest influence on the exponent c of the Pareto type II mass spectra (Figs 1c,d & 5).

Many size-related variables were strongly correlated (Table 2). To avoid redundant information, we selected for further analyses only those variables with Spearman's $r < |0.6|$ in correlations or those that contained most information from the original data. Accordingly, size diversity (SD) was favoured over L_{gmean} (correlation with SD: $r_s = 0.69$), L_{var} ($r_s = 0.83$), L_{skew} ($r_s = -0.75$), L_{kurt} ($r_s = -0.66$), IQR ($r_s = 0.82$), L_{95} ($r_s = 0.76$) and L_{qual} ($r_s = 0.71$) because size diversity contains information on the amplitude of the size range and the relative distribution of sizes along the size range (Quintana *et al.*, 2008). Furthermore, strong correlations existed between those variables that we decided to exclude in favour of size diversity (Table 2). The number of size classes (n SC) was only strong correlated with L_{qaul}, which was already excluded. Maximum length and the condition factor of the fish assemblage were not correlated with any other size-related variable ($r_s < 0.55$). In the

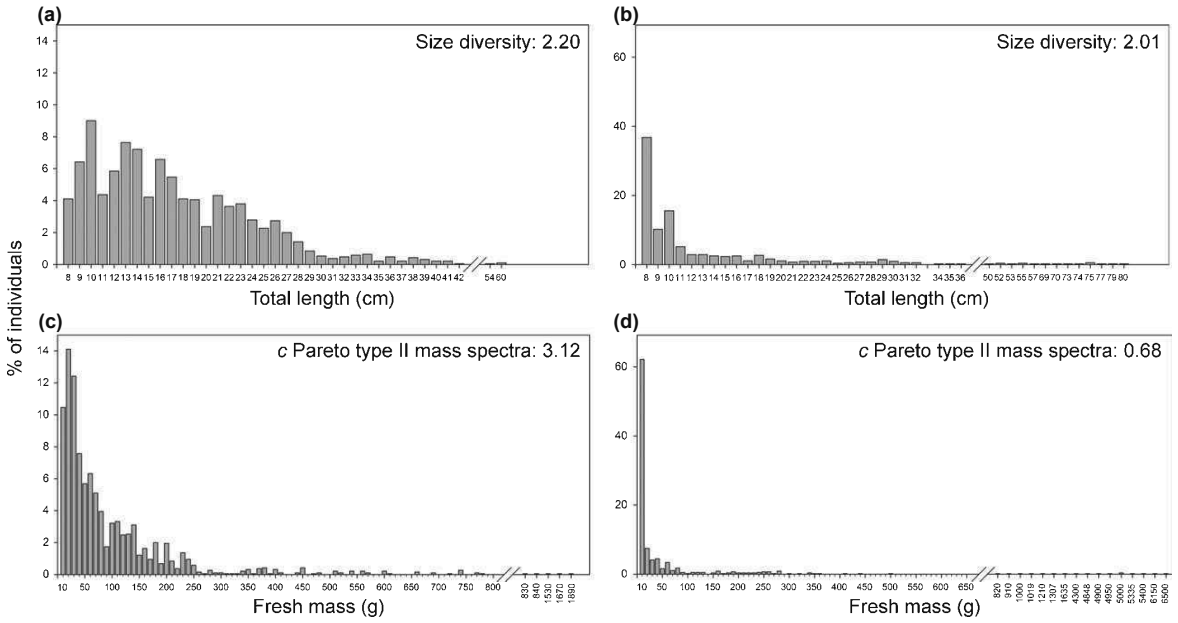

Fig. 1 Examples of fish-length distributions from two lakes with similar values of size diversity (a, b) and their corresponding mass distributions with substantial differences in their exponents *c* of the Pareto type II mass distributions (c, d).

case of normalised length and mass-spectra slopes (r_s = 0.91), we selected the slopes of the normalised length spectra over the ones of the mass spectra because parameters of the Pareto type II mass spectra also described the mass distribution. No classification or transformation of the mass data is necessary in the Pareto approach (Blanco, Echevarria & Garcia, 1994; Vidondo *et al.*, 1997). The mass of each individual fish was included in the calculations resulting in a higher mean R^2 value (0.97) in comparison with the mean R^2 of the normalised mass spectra (0.86). We selected only the exponent *c* of the Pareto type II mass spectra, because the additive constant *D* was highly redundant (correlations with *c*: r_s = 0.83; IQR: r_s = 0.66).

Ultimately, eight size-related variables were included in the main matrix and exposed to a NMDS analysis: number of size classes, maximum length, Fulton's condition factor, parameter *c* and R^2 of the Pareto type II mass spectra, slope and R^2 of the normalised length spectra and size diversity.

The NMDS analysis on eight size-related variables resulted in a three-dimensional solution (Fig. 2; final stress = 6.84, final instability = 0.00001 at 164 iterations). The three axes accounted for 96.8% of the variation. The first axis (15.6% predicted variance) was negatively correlated with the number of size classes (Spearman's $r = -0.79$). The second axis (40.8%) was negatively correlated with the slope of the normalised length spectra ($r_s = -0.88$) and size diversity ($r_s = -0.64$). The third axis (40.4%) was negatively correlated with the exponent *c* of the Pareto type II mass spectra ($r_s = -0.65$) and positively correlated with maximum length (r_s = 0.73). All other size-related variables were less strongly correlated with the NMDS axes ($r_s < |0.53|$).

Ordination of lake-use intensity variables

The first two axes of the MCA explained 32.7% of the predicted variance (axis 1: 20.6% and axis 2: 12.1%). Axis 1 was strongly correlated with the frequency of footbridges/marinas (Spearman's r = 0.85), the frequency of recreational boats with and without engines (r_s = 0.74 and r_s = 0.76), bathing places (r_s = 0.74) and bathing activities (r_s = 0.73). The second axis was correlated with the frequency of footbridges/marinas (r_s = 0.47), types of fishing activities (r_s = 0.45), frequency of fascines (r_s = 0.41) and sheet piles (r_s = 0.42). The scores of lakes on these two axes were included in the comatrix of abiotic lake descriptors for the NMDS analysis.

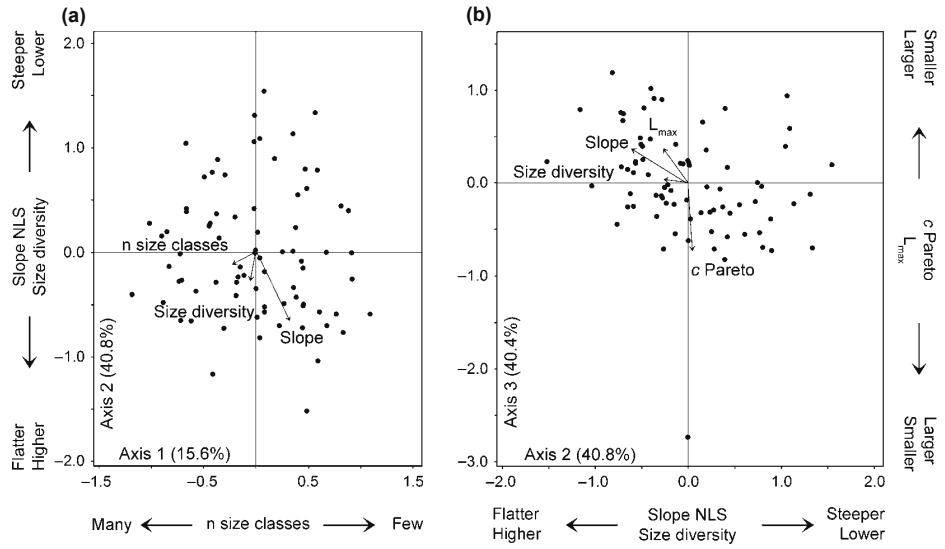

Fig. 2 Plots obtained from non-metric multidimensional scaling analysis based on eight size-related variables derived from fish assemblages of 78 lakes sampled with multi-mesh gillnets. Two plots of the three-dimensional solution (96.8% predicted variance) are shown (predicted variance in brackets): Axis 1 vs. axis 2 (a) and axis 2 vs. axis 3 (b), both including correlation vectors of significant size-related variables with Spearman's $r > |0.60|$. For better illustration, vectors were enlarged to 400%. Interpretation of the axes scores are given on the horizontal and vertical axes. The slope was calculated from normalised length spectra (NLS), the exponent c was calculated from Pareto type II mass spectra; L_{max} = maximum length.

Response of size-related variables along gradients

Fifteen variables from three groups of lake and fish-assemblage descriptors were strongly correlated (Spearman's $r > |0.30|$, $P \leq 0.004$) with the axes of the NMDS analysis on size-related variables (Table 3; Figs 3–5), thus reflecting correspondence of size-related variables to lake morphometry, lake productivity and functional fish-assemblage composition.

The number of size classes increased with increasing lake area and decreased with increasing mean depth (Fig. 3a,b). Furthermore, more size classes were observed in lakes with larger catchment areas and lakes with more species caught in the gillnets (Fig. 3c,d). The slopes of the normalised length spectra were flatter (i.e. less negative = fewer small, more large fish or both), and size diversity was higher in deep lakes (Fig. 4a,b) and in lakes with lower nutrient concentrations (Fig. 4c,d). Additionally, flatter slopes and higher size diversity were observed where the numerical abundance of piscivorous fish was high (Fig. 4e). The exponent c of the Pareto type II mass spectra was larger (i.e. a higher relative proportion of medium-sized fish), and the maximum observed fish length in the gillnets was smaller in shallow (Figs 5a,b & 6a; Table 4a) and nutrient-rich lakes (Figs 5c,d & 6a; Table 4a). A higher proportion of predator biomass and higher predator/prey length ratios (influenced by a strong increase in arithmetic mean predator lengths but only a slight decrease in mean prey lengths, M. Emmrich unpublished) were associated with smaller exponents and larger maximum lengths (Figs 5e,f & 6d; Table 4d).

Discussion

The comparison of 18 size-related variables derived from multimesh gillnet catches from 78 German lowland lakes showed substantial variation, even within a data set limited in geographical range. Many of the variables were strongly correlated. An ordination of the lakes, based on eight weakly correlated size descriptors with slope of normalised length spectra, size diversity, exponent c of Pareto type II mass spectra, maximum length and number of size classes as the most important ones, was correlated with descriptors of lake morphometry, lake productivity and functional fish-assemblage composition. This suggests that size spectra can be a useful tool for identifying systematic variation in fish assemblages along environmental gradients.

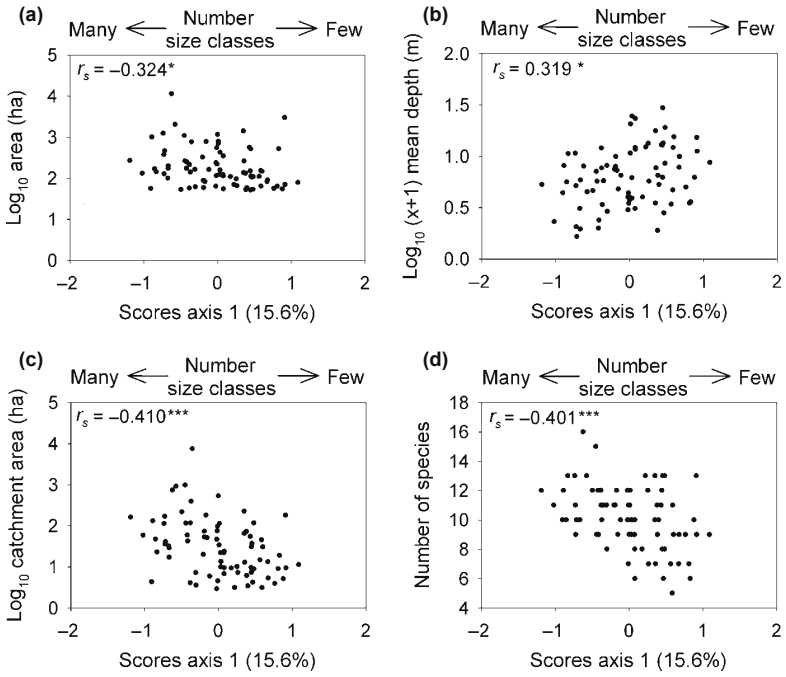

Fig. 3 Scatter plots of correlated (Spearman's $r > |0.30|$) variables with the scores of axis 1 of the non-metric multidimensional scaling analysis based on eight size-related variables. Interpretation of the axes scores are given on the top horizontal axes. Spearman rank correlation coefficients (r_s) and level of significance are given in addition (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

Lake area was positively correlated with the number of size classes, indicating a wider range of fish sizes with more large sizes in large lakes. Similarly, Sumari (1971) found more size classes of perch in larger ponds. Our results are also in accordance with empirical studies (Holmgren & Appelberg, 2000; Wilde & Pope, 2004) supporting the theory that larger lakes are inhabited by larger fish. As for European lakes in general (Nõges, 2009), lake area was positively correlated with catchment area in our study (Pearson's r for $\log_{10}$-transformed lake and catchment area: 0.66; $P < 0.001$). Additionally, species richness in the gillnets was correlated with lake area ($r = 0.36$; $P = 0.001$; cf. Eckmann, 1995). We conclude that the correlation of catchment area and species richness with axis 1 of the NMDS analysis was a consequence of their positive correlations with lake size. As we included only lakes >50 ha in our study, we cannot preclude the possibility that lake area becomes more important for other size-related variables if smaller lakes are considered as well.

In addition to lake area, we showed also that lake depth influenced the size structure of fish assemblages, because depth-related variables were correlated with all significant size variables. In lakes of greater mean depth, fewer size classes were found, which contradicts our initial assumption that deeper lakes would be associated with a higher diversity of fish size. Deeper lakes are often associated with higher habitat heterogeneity, thus reducing competition and providing habitat for more different age (size) classes (Persson, 1983). The opposite results from the different studies suggest that the correspondence between lake depth and number of size classes has to be reanalysed in a larger data set.

The second axis of the NMDS analysis was negatively correlated with the slope of the normalised length spectra and size diversity. Both size metrics showed similar responses to variables of lake depth, nutrient concentrations and predator abundance, because the slope of normalised length spectra and size diversity identify patterns in the relative proportion of small and large fish in the catches. Flatter (less negative) slopes indicate fewer small fish, more large fish or both (Pope & Knights, 1982; Bianchi *et al.*, 2000). Higher values of size diversity are obtained if the relative proportion of large fish is higher, which is supported by the strong correlation of size diversity with L_{gmean}, L_{var}, IQR and the strong correlations with variables directly corresponding to large fish in the catches (L_{qual} and L_{95}).

Deep lakes, and lakes with lower nutrient concentrations and a higher numerical proportion of predators, have flatter slopes and higher size diversity. This

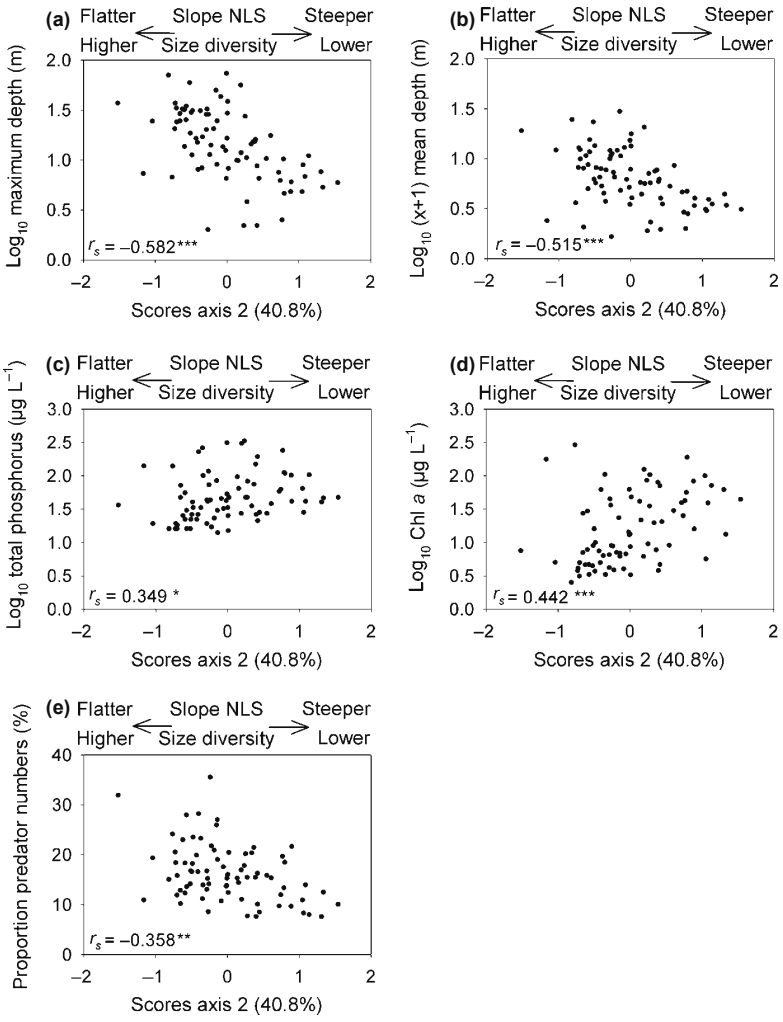

Fig. 4 Scatter plots of correlated (Spearman's $r > |0.30|$) variables with the scores of axis 2 of the non-metric multidimensional scaling analysis based on eight size-related variables. Interpretation of the axes scores are given on the top horizontal axes. Spearman rank correlation coefficients (r_s) and level of significance are given in addition (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Slope NLS: slope of normalised length spectra.

suggests either a lower survival rate of small fish or a higher abundance of large fish in those lakes. Although a high abundance of predators is characteristic of deep, mesotrophic lakes (Persson *et al.*, 1991; Jeppesen *et al.*, 2000), Mehner (2010) recently failed to demonstrate a negative relationship between the abundance of piscivorous fish and their potential prey in German lakes. Accordingly, we conclude that flatter slopes and higher values of size diversity are primarily caused by a high proportion of large fish rather than indicating high mortality rates of small fish because of predation. However, the single effects of predators on the size structure of fish assemblages were somewhat difficult to disentangle because we included both predatory and prey fish in calculations of the size-related variables. Therefore, the observed patterns reflect in part the positive correlation between the abundance of large fish (42% of all fish >30 cm were classified as predators) and flatter slopes and higher size-diversity values. Nevertheless, we suggest that predation is one of the major forces shaping the size structure of lake fish assemblages (Jackson, Peres-Neto & Olden, 2001; Kerr & Dickie, 2001) even if no negative abundance relationship can be found (Mehner, 2010). Further studies are needed to analyse in detail the impact of piscivorous fish (i.e. the abundance and size of predators) on the size structure of the total fish assemblage and their potential prey.

The exponent c of the Pareto type II mass spectra and maximum length were correlated with six lake and fish-assemblage variables. Exponents were largest

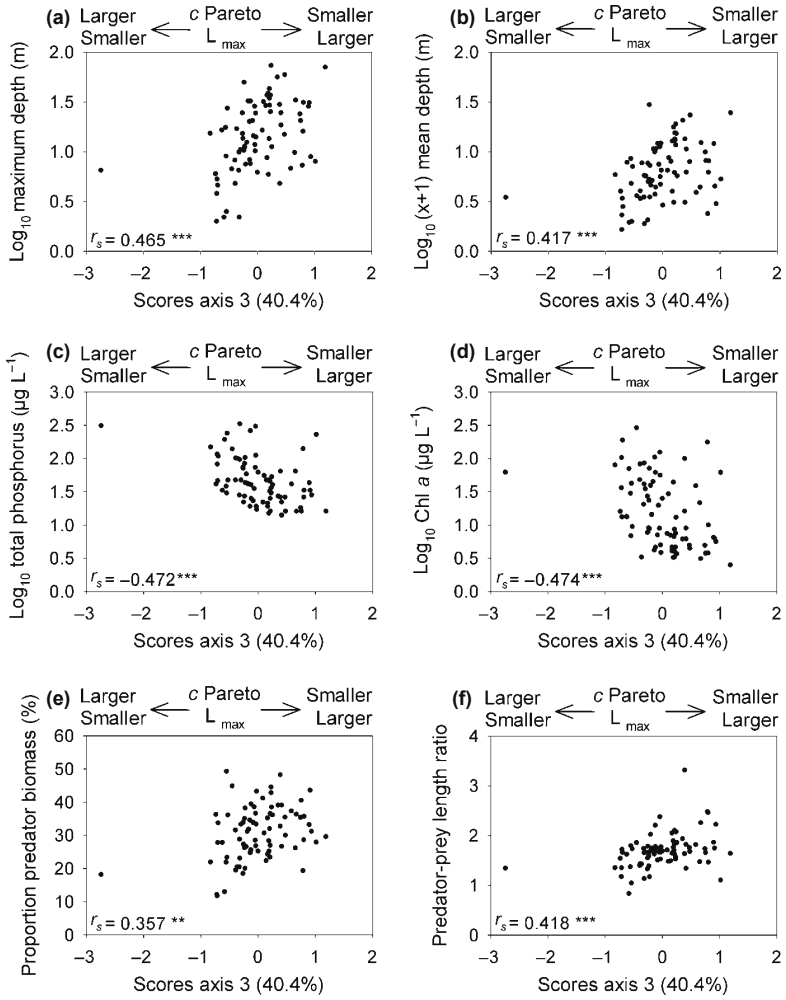

Fig. 5 Scatter plots of correlated (Spearman's $r > |0.30|$) variables with the scores of axis 3 of the non-metric multidimensional scaling analysis based on eight size-related variables. Interpretation of the axes scores are given on the top horizontal axes. Spearman rank correlation coefficients (r_s) and level of significance are given in addition (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).
c Pareto: exponent of the Pareto type II mass spectra, L_{max} = maximum length.

if the size range of the gillnet catch was narrow and characterised by a more even distribution of fish mass, with a greater relative abundance of medium-sized fish. According to axis 3 of the NMDS analysis, we found smaller maximum fish lengths and a higher relative proportion of medium-sized fish in shallow, nutrient-rich lakes. The correlation between lake morphometry and nutrient status is characteristic of European lakes (Nõges, 2009), because rapid nutrient recycling in the extensive littoral zone favours higher productivity (Ryder, 1965; Hanson & Leggett, 1982). The relative increase in medium-sized fish contradicts in part the results of Jeppesen *et al.* (2000), who found a decline in mean body mass of the dominant fish species perch, roach [*Rutilus rutilus* (L.)] and bream [*Abramis brama* (L.)] in Danish lakes along an increasing nutrient gradient. However, the Danish lakes were on average shallower (mean depth 3.4 m) than the lakes in our study (6.9 m), suggesting weaker interaction strengths in German lakes. At a given nutrient concentration, volumetric fish densities and productivity decline with increasing lake depth (Ryder, 1965; Jeppesen *et al.*, 1997), thus reducing the interaction strength in deeper lakes (Jeppesen *et al.*, 1997) as a consequence of reduced habitat coupling, which is primarily mediated by fish (Jackson *et al.*, 2001; Schindler & Scheuerell, 2002; Dolson *et al.*, 2009). Furthermore, the exponent *c* was smaller where predator biomass and predator/prey length ratios were large. An increase in the predator/prey length ratio was primarily caused by an increase in predator length. Consequently, a few large predators with a high biomass have a limited regulatory impact on the many small fish.

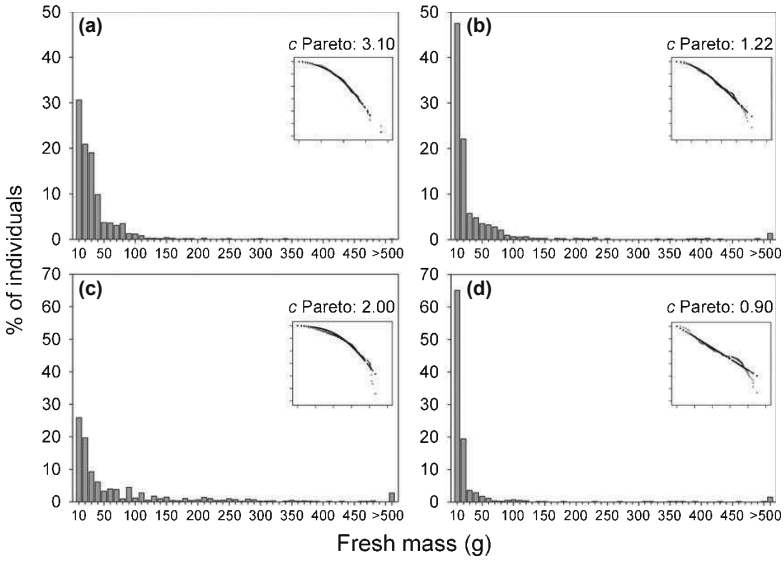

Fig. 6 Four examples of mass distributions and exponents *c* of their corresponding Pareto type II mass spectra (insets) of lake fish assemblages sampled with multi-mesh gillnets. The lakes differed in those descriptors that were significantly correlated with the lake scores derived from the non-metric multidimensional scaling analysis (cf. Fig. 5; Table 4): (a): shallow, nutrient-rich lake; (b): deep, less nutrient-rich lake; (c): low predator biomass, low predator-prey length ratio (PPLR); (d): high predator biomass, high PPLR.

Table 4 Descriptors of lake morphometry, lake productivity and functional fish-assemblage composition of the four example lakes whose fish-mass distributions are shown in Fig. 6. Significant differences in lake descriptors are indicated in boldface. (a) Shallow, nutrient-rich lake; (b) deep, less nutrient-rich lake; (c) low predator biomass, low predator/prey length ratio (PPLR); (d) high predator biomass, high PPLR

Lake	(a)	(b)	(c)	(d)
Maximum depth (m)	**5.0**	**19.1**	6.5	6.1
Mean depth (m)	**3.0**	**8.9**	1.3	2.1
Total phosphorus (μg L^{-1})	**40.0**	**18.0**	81.0	63.0
Chlorophyll *a* (μg L^{-1})	**15.9**	**3.2**	102.0	98.4
Predator biomass (%)	36.3	34.6	**11.8**	**48.2**
PPLR	1.54	1.63	**1.3**	**3.3**

Maximum fish length increased with increasing lake depth and decreasing nutrient concentration. It has been argued that sample size and sampling effort determine the maximum length of fish caught (Shin *et al.*, 2005). We found no correlation between maximum fish length and the number of fish caught or the number of nets set. Nevertheless, it has been shown that very large fish are not adequately represented in multimesh gillnets if only the standard effort is applied (Holmgren & Appelberg, 2000; Pope, Wilde & Bauer, 2005), which makes a coherent interpretation of this size metric more difficult. However, although large fish in lakes have larger home ranges (Minns, 1995), the probability of catching them in large, deep lakes will certainly not increase, because the very large pelagic zone is only poorly sampled by gillnets (Deceliere-Verges & Guillard, 2008). Consequently, we can assume that deeper lakes are inhabited by more fish of a maximum size. Wilde & Pope (2004) argued that large fish are less vulnerable to exploitation in large lakes, and it has been shown that fishing pressure can act as a major force shaping the size structure of lake fish assemblages (McDonald & Hershey, 1989; Lewin, Arlinghaus & Mehner, 2006). We did not detect any significant effect of fishing on any size variable. However, the quantification of fishing activity was based on a ranked scale that determined only the type of fishing (commercial or recreational) and not its intensity. Accordingly, we cannot exclude the possibility that the four categories were too coarse to detect subtle impacts of fishing on size structure.

In addition to fishing pressure, the impact of shoreline modifications and the intensity of recreational activities had no influence on size structure. The effects of lake morphometry and nutrient status, both important in determining habitat complexity and habitat availability for fish, had a much stronger impact on the size structure compared with anthropogenic effects of shoreline development and recreational activities. We suggest that the categorical data on lake-use intensity are not sufficiently sensitive to detect the changes in size structure and that the degree of anthropogenic degradation of the German lakes is too low (Mehner *et al.*, 2005) to impact size structure significantly.

In summary, the application of size-related variables to multimesh gillnet catches is a promising tool that can provide important information on systematic shifts in the size structure of lake fish assemblages along environmental gradients. In particular, the measure of size diversity might be a powerful tool for analysing fish size distributions as it condenses many different aspects of other size metrics into a single comparable value. The exponent *c* of the Pareto type II mass spectra uncovers differences in the relative abundances of small- and medium-sized fish. However, we recommend the visualisation of size distributions (for instance in the form of size-frequency histograms) to complement the interpretation of results of the size metrics, because similar values can be obtained from different underlying size distributions. Our results suggest that the more frequent use of size-based approaches could help in evaluating the ecological status of lakes. Further studies including a broader range of environmental and geographical gradients would be beneficial for analysing the subtle response of size-related variables of fish assemblages.

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References

Appelberg M. (2000) Swedish standard methods for sampling freshwater fishes with multi-mesh gill nets. *Fiskeriverket Information*, **1**, 1–32.

Arend K.K. & Bain M.B. (2008) Fish communities in coastal freshwater ecosystems: the role of the physical and chemical setting. *BioMed Central Ecology*, **8**, 23.

Beier U. (2001) Habitat distribution and size structure in freshwater fish communities: effects of vendace on interactions between perch and roach. *Journal of Fish Biology*, **59**, 1437–1454.

Bianchi G., Gislason H., Graham K., Hill L., Jin X., Koranteng K. *et al.* (2000) Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science*, **57**, 558–571.

Blanchard J.L., Dulvy N.K., Jennings S., Ellis J.R., Pinnegar J.K., Tidd A. *et al.* (2005) Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? *ICES Journal of Marine Science*, **62**, 405–411.

Blanchard J.L., Jennings S., Law R., Castle M.D., McCloghrie P., Rochet M.J. *et al.* (2009) How does abundance scale with body size in coupled size-structured food webs? *Journal of Animal Ecology*, **78**, 270–280.

Blanco J.M., Echevarria F. & Garcia C.M. (1994) Dealing with size spectra: some conceptual and mathematical problems. *Scientia Marina*, **58**, 17–29.

Brucet S., Quintana X.D., Moreno-Amich R. & Boix D. (2005) Changes in the shape of zooplankton biomass-size spectra at ecological scaling in a fluctuating ecosystem (Emporda wetlands, NE Spain). *Vie et Milieu*, **55**, 31–40.

Brucet S., Boix D., Quintana X.D., Jensen E., Nathansen L.W., Trochine C. *et al.* (2010) Factors influencing zooplankton size structure at contrasting temperatures in coastal shallow lakes: Implications for effects of climate change. *Limnology and Oceanography*, **55**, 1697–1711.

Calder W.A. (1984) *Size Function and Life History*. Harvard University Press, Cambridge.

CEN (European Committee for Standardisation) (2005) *EN 14757. Water Quality – Sampling of Fish with Multi-Mesh Gill Nets*. CEN (European Committee for Standardisation), Brussels.

Choi J.S., Mazumder A. & Hansell R.I.C. (1999) Measuring perturbation in a complicated, thermodynamic world. *Ecological Modelling*, **117**, 143–158.

De Leeuw J.J., Nagelkerke L.A.J., Van Densen W.L.T., Holmgren K., Jansen P.A. & Vijverberg J. (2003) Biomass size distributions as a tool for characterizing lake fish communities. *Journal of Fish Biology*, **63**, 1454–1475.

Deceliere-Verges C. & Guillard J. (2008) Assessment of the pelagic fish populations using CEN multi-mesh gillnets: consequences for the characterization of the fish communities. *Knowledge and Management of Aquatic Ecosystems*, **389**, 4.

Diekmann M., Brämick U., Lemcke R. & Mehner T. (2005) Habitat-specific fishing revealed distinct indicator species in German lowland lake fish communities. *Journal of Applied Ecology*, **42**, 901–909.

Dolson R., McCann K., Rooney N. & Ridgway M. (2009) Lake morphometry predicts the degree of habitat coupling by a mobile predator. *Oikos*, **118**, 1230–1238.

Eckmann R. (1995) Fish species richness in lakes of the northeastern lowlands in Germany. *Ecology of Freshwater Fish*, **4**, 62–69.

Gamble A.E., Lloyd R., Aiken J., Johannsson O.E. & Mills E.L. (2006) Using zooplankton biomass size spectra to assess ecological change in a well-studied freshwater lake ecosystem: Oneida Lake, New York. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 2687–2699.

Godlewska M. & Świerzowski A. (2003) Hydroacoustical parameters of fish in reservoirs with contrasting levels of eutrophication. *Aquatic Living Resources*, **16**, 167–173.

Greenacre M.J. & Blasius J. (2006) *Multiple Correspondence Analysis and Related Methods*. Chapman & Hall/CRC, Boca Raton.

Griffiths D. (2006) The direct contribution of fish to lake phosphorus cycles. *Ecology of Freshwater Fish*, **15**, 86–95.

Hanson J.M. & Leggett W.C. (1982) Empirical prediction of fish biomass and yield. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**, 257–263.

Holmgren K. (1999) Between-year variation in community structure and biomass-size distributions of benthic lake fish communities. *Journal of Fish Biology*, **55**, 535–552.

Holmgren K. & Appelberg M. (2000) Size structure of benthic freshwater fish communities in relation to environmental gradients. *Journal of Fish Biology*, **57**, 1312–1330.

Illies J. (1978) *Limnofauna Europaea*. Gustav Fischer. Stuttgart, Germany.

Jackson D.A., Peres-Neto P.R. & Olden J.D. (2001) What controls who is where in freshwater fish communities – The roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 157–170.

Jennings S. & Dulvy N.K. (2005) Reference points and reference directions for size-based indicators of community structure. *ICES Journal of Marine Science*, **62**, 397–404.

Jennings S., Pinnegar J.K., Polunin N.V.C. & Boon T.W. (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, **70**, 934–944.

Jeppesen E., Jensen J.P., Søndergaard M., Lauridsen T., Pedersen L.J. & Jensen L. (1997) Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia*, **342**, 151–164.

Jeppesen E., Jensen J.P., Søndergaard M., Lauridsen T. & Landkildehus F. (2000) Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwater Biology*, **45**, 201–218.

Kerr S.R. & Dickie L.M. (2001) *The Biomass Spectrum: A Predator-Prey Theory of Aquatic Production*. Columbia University Press, New York.

Kruskal J.B. (1964) Nonmetric multidimensional scaling: a numerical method. *Psychometrika*, **29**, 115–129.

Kurkilahti M. & Rask M. (1996) A comparative study of the usefulness and catchability of multimesh gill nets and gill net series in sampling of perch (*Perca fluviatilis* L) and roach (*Rutilus rutilus* L). *Fisheries Research*, **27**, 243–260.

Lewin W.C., Arlinghaus R. & Mehner T. (2006) Documented and potential biological impacts of recreational fishing: insights for management and conservation. *Reviews in Fisheries Science*, **14**, 305–367.

McCune B. & Mefford M.J. (1999) *PC-ORD. Multivariate Analysis of Ecological Data, Version 4*. MjM Software Design, Gleneden Beach, Oregon.

McDonald M.E. & Hershey A.E. (1989) Size structure of a lake trout (*Salvelinus namaycush*) population in an arctic lake: Influence of angling and implications for fish community structure. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 2153–2156.

Mehner T. (2010) No empirical evidence for community-wide top-down control of prey fish density and size by fish predators in lakes. *Limnology and Oceanography*, **55**, 203–213.

Mehner T., Diekmann M., Brämick U. & Lemcke R. (2005) Composition of fish communities in German lakes as related to lake morphology, trophic state, shore structure and human-use intensity. *Freshwater Biology*, **50**, 70–85.

Mehner T., Holmgren K., Lauridsen T.L., Jeppesen E. & Diekmann M. (2007) Lake depth and geographical position modify lake fish assemblages of the European 'Central Plains' ecoregion. *Freshwater Biology*, **52**, 2285–2297.

Minns C.K. (1995) Allometry of home-range size in lake and river fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1499–1508.

Nenadić O. & Greenacre M. (2007) Correspondence analysis in R, with two- and three-dimensional graphics: the ca package. *Journal of Statistical Software*, **20**, 3.

Nõges T. (2009) Relationships between morphometry, geographic location and water quality parameters of European lakes. *Hydrobiologia*, **633**, 33–43.

Olin M. & Malinen T. (2003) Comparison of gillnet and trawl in diurnal fish community sampling. *Hydrobiologia*, **506**, 443–449.

Olin M., Rask M., Ruuhijärvi J., Kurkilahti M., Ala-Opas P. & Ylonen O. (2002) Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. *Journal of Fish Biology*, **60**, 593–612.

Olin M., Kurkilahti M., Peitola P. & Ruuhijärvi J. (2004) The effects of fish accumulation on the catchability of multimesh gillnet. *Fisheries Research*, **68**, 135–147.

Olin M., Malinen I. & Ruuhijärvi J. (2009) Gillnet catch in estimating the density and structure of fish community-Comparison of gillnet and trawl samples in a eutrophic lake. *Fisheries Research*, **96**, 88–94.

Persson L. (1983) Food consumption and competition between age classes in a perch *Perca fluviatilis* population in a shallow eutrophic lake. *Oikos*, **40**, 197–207.

Persson L., Diehl S., Johansson L., Andersson G. & Hamrin S.F. (1991) Shifts in fish communities along the productivity gradient of temperate lakes – patterns and the importance of size-structured interactions. *Journal of Fish Biology*, **38**, 281–293.

Persson L., Diehl S., Johansson L., Andersson G. & Hamrin S.F. (1992) Trophic interactions in temperate lake ecosystems – a test of food-chain theory. *The American Naturalist*, **140**, 59–84.

Petchey O.L. & Belgrano A. (2010) Body-size distributions and size spectra: universal indicators of ecological status? *Biology Letters*, **6**, 434–437.

Peters R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.

Pope J.G. & Knights B. (1982) Comparison of the length distributions of combined catches of all demersal fishes in surveys in the North Sea and at Faroe Bank. In: *Canadian Special Publication of Fisheries and Aquatic Sciences*, (ed Mercer M.C.) *Multispecies Approaches to Fisheries Management*, **59**, 116–118.

Pope K.L., Wilde G.R. & Bauer D.L. (2005) Maximum size of fish caught with standard gears and recreational angling. *Fisheries Research*, **76**, 117–122.

Post J.R., Parkinson E.A. & Johnston N.T. (1999) Density-dependent processes in structured fish populations: Interaction strengths in whole-lake experiments. *Ecological Monographs*, **69**, 155–175.

Prchalová M., Kubečka J., Řiha M., Mrkvčika T., Vašek M., Jůza T. *et al*. (2009) Size selectivity of standardized multimesh gillnets in sampling coarse European species. *Fisheries Research*, **96**, 51–57.

Prchalová M., Mrkvčika T., Peterka J., Čech M., Berec L. & Kubečka J. (2011) A model of gillnet catch in relation to the catchable biomass, saturation, soak time and sampling period. *Fisheries Research*, **107**, 201–209.

Quintana X.D., Brucet S., Boix D., López-Flores R., Gascón S., Badosa A. *et al*. (2008) A nonparametric method for the measurement of size diversity with emphasis on data standardization. *Limnology and Oceanography, Methods*, **6**, 75–86.

R Development Core Team (2008) *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Wien. URL http://www.R-project.org.

Rochet M.J. & Trenkel V.M. (2003) Which community indicators can measure the impact of fishing? A review and proposals. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 86–99.

Roff A. (1992) *The Evolution of Life Histories. Theory and Analysis*. Chapman & Hall, New York.

Ryder R.A. (1965) A method for estimating the potential fish production of north-temperate Lakes. *Transactions of the American Fisheries Society*, **94**, 214–218.

Schindler D.E. & Scheuerell M.D. (2002) Habitat coupling in lakes ecosystems. *Oikos*, **98**, 177–189.

Sheldon R.W., Prakash A. & Sutcliffe W.H. (1972) The size distribution of particles in the ocean. *Limnology and Oceanography*, **17**, 327–340.

Shin Y.J. & Cury P. (2004) Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 414–431.

Shin Y.J., Rochet M.J., Jennings S., Field J.G. & Gislason H. (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science*, **62**, 384–396.

Sokal R.R. & Rohlf F.J. (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd edn. W.H. Freeman, New York.

Sprules W.G. & Munawar M. (1986) Plankton size spectra in relation to ecosystem productivity, size, and perturbation. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1789–1794.

Sprules W.G., Casselman J.M. & Shuter B.J. (1983) Size distribution of pelagic particles in lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 1761–1769.

Strayer D.L. (1991) Perspectives on the size structure on lacustrine zoobenthos, its causes, and its consequences. *Journal of the North American Benthological Society*, **10**, 210–221.

Sumari O. (1971) Structure of the perch population of some ponds in Finland. *Annales Zoologici Fennici*, **8**, 406–421.

Sweeting C.J., Badalamenti F., D'Anna G., Pipitone C. & Polunin N.V.C. (2009) Steeper biomass spectra of demersal fish communities after trawler exclusion in Sicily. *ICES Journal of Marine Science*, **66**, 195–202.

Tammi J., Appelberg M., Beier U., Hesthagen T., Lappalainen A. & Rask M. (2003) Fish status survey of Nordic lakes: effects of acidification, eutrophication and stocking activity on present fish species composition. *Ambio*, **32**, 98–105.

Tenenhaus M. & Young F.W. (1985) An analysis and synthesis of multiple correspondence-analysis, optimal-scaling, dual scaling, homogeneity analysis and other methods for quantifying categorical multivariate data. *Psychometrika*, **50**, 91–119.

Tonn W.M., Magnuson J.J., Rask M. & Toivonen J. (1990) Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. *The American Naturalist*, **136**, 345–375.

Vidondo B., Prairie Y.T., Blanco J.M. & Duarte C.M. (1997) Some aspects of the analysis of size spectra in aquatic ecology. *Limnology and Oceanography*, **42**, 184–192.

Wellborn G.A., Skelly D.K. & Werner E.E. (1996) Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics*, **27**, 337–363.

Werner E.E. & Gilliam J.F. (1984) The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology and Systematics*, **15**, 393–425.

Wilde G.R. & Pope K.L. (2004) Relationship between lake-record weights of fishes and reservoir area and growing season. *North American Journal of Fisheries Management*, **24**, 1025–1030.

Winiwarter P. & Cempel C. (1992) Life symptoms: the behaviour of open systems with limited energy dissipation capacity and evolution. *Systems Research*, **9**, 9–34.

Ylikarjula J., Heino M. & Dieckmann U. (1999) Ecology and adaptation of stunted growth in fish. *Evolutionary Ecology*, **13**, 433.

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Paper V

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Temperature-related effects on life history and species composition induce major shifts in size structure of European lake fish assemblages

Manuscript

Temperature-related effects on life history and species composition induce major shifts in size structure of European lake fish assemblages

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Running head: size structure of European lake fish assemblages

Summary

1) Organism body size has a strong effect on the structure and function of ecosystems because many ecological and physiological processes such as predator-prey interactions, size-abundance relationships and energy fluxes in food webs are highly size-dependent. Understanding the predictors of the size structure of assemblages is essential for identifying and predicting the response of species assemblages and ecosystems to anthropogenic disturbances and environmental change.
2) We analysed the size structure of fish assemblages by calculating average size, maximum size and the individual size distribution from fish sampled by standardised gillnetting in 701 European lakes. Variation in the size metrics was explored in relation to the lakes' location, morphometry, trophic status and fish assemblage composition using boosted regression tree analysis.
3) Two fundamentally different types of size structure were identified. The majority of the lakes, mainly located in the European lowlands, was characterised by a dominance of small-sized juvenile perch or roach. Lakes at higher elevation at either high or low latitudes with salmonid-dominated fish assemblages were characterised by more large-sized fish and low abundances of juvenile fish. Trophic status of the lakes had no significant influence on variation in the size structure across this large geographical scale, presumably because its effect was overridden by temperature effects.
4) A switch in the dominant life-history strategy and thereby the taxonomic composition from equilibrium type in salmonids to periodic type in cyprinids and percids is accompanied by a marked shift in the size structure of lake fish assemblages. Temperature is a main predictor of these size shifts and therefore strong effects on lake ecosystem functioning can be expected from future global warming.

Keywords: biogeography, body size, lake, freshwater fish, life history, multi-mesh gillnet, individual size distribution, latitudinal gradient, salmonid, size spectra

Introduction

The importance of organism body size on the structure and function of ecosystems has long been recognised (Elton 1927; Peters 1983; Kerr & Dickie 2001). Various ecological and physiological processes such as respiration, growth, maturation, reproduction and life span are strongly size-dependent (Blueweiss *et al.* 1978; Calder 1984). Variations in body size has a significant effect across multiple levels of ecosystem organisation, and determine predator-prey interactions, body-size abundance relationships and energy fluxes in food webs (Emmerson & Raffaelli 2004; Reuman & Cohen 2005; Woodward *et al.* 2005; White *et al.* 2007). Exploring the drivers of the size structure of assemblages is important not only for the understanding and identification of fundamental ecological processes, but also for identifying and predicting the response of species assemblages and ecosystems to anthropogenic disturbances and environmental change (Petchey & Belgrano 2010; Yvon-Durocher *et al.* 2011; Gardner *et al.* 2011).

The size structure of organism assemblages has been analysed for various terrestrial and aquatic ecosystem types (for summary see e.g. Yvon-Durocher *et al.* 2011). Most studies have been conducted in marine ecosystems, and investigated fishing impacts on commercially important fish stocks (e.g. Bianchi *et al.* 2000; Blanchard *et al.* 2009). Substantially less is known about factors which modify the size structure of lake fish assemblages, particularly across large geographical scales (Emmrich *et al.* 2011). Empirical evidence from a few regional studies indicates that differences in fish size distributions can be explained by differences in lake morphometry, lake productivity and functional fish assemblage composition (Jeppesen *et al.* 2000; Holmgren & Appelberg 2000; Jeppesen *et al.* 2010; Emmrich *et al.* 2011). Local presence/absence data and maximum species-specific fish size are taken from the scientific literature and have been used to analyse changes in species richness across size classes over large geographical scales (Lindsey 1966; Knouft 2004; Griffiths 2010). Other studies have focused on selected species and have demonstrated variations in fish body size across latitudinal gradients (Heibo, Magnhagen, & Vøllestad 2005; Blanck & Lamouroux 2007; Lappalainen, Tarkan, & Harrod 2008). These results demonstrated that fish assemblages in warm environments typically consist of more small-sized species (Knouft 2004; Teixeira-de Mello *et al.* 2009; Griffiths 2010), and individuals of the same species are larger in cold environments than conspecifics in warm environments (Blanck & Lamouroux 2007; Lappalainen *et al.* 2008; Jeppesen *et al.* 2010). Accordingly, the size of ectothermic animals is temperature-dependent resulting from physiological constraints at extreme temperatures (Lindsey 1966; Atkinson & Sibly 1997). Despite previous studies, it remains unresolved how much the size structure of entire lake fish assemblages varies over large spatial scales, and what are the main predictors of this variation. For this endeavour, ideally, relative abundances of local species obtained from standardised samplings can

be merged with individual fish size measures, and combined with a range of lake variables related to morphometry, productivity and geographic location. Such large datasets from lakes were not previously available.

In this study, we moved beyond previous approaches in three directions. Firstly, we used a large dataset including fish catches from 701 lakes located in eight countries which cover a latitudinal range of 28° and a longitudinal range of 35° across Europe. Fish assemblages were sampled with standardised benthic multi-mesh gillnets and evaluated with respect to species, individual body length and mass. Secondly, we compared predictions from previously published regional studies on the correspondence between size structure differences and environmental gradients with the empirical results obtained from our large-scale dataset. We compared the slopes of individual size distributions (ISD) (*sensu* size spectra, White *et al.* 2007), and average and maximum size of the fish assemblages along geographic and thermal gradients, gradients of lake morphometry and variations in lake productivity. Thirdly, we included biotic predictors which characterise taxonomic fish assemblage composition to account for potential species shifts along the abiotic gradients in this large-scale analysis.

According to previous studies, we expected the following patterns: Average size of the fish assemblage is predicted to increase with increasing latitude, elevation and lake depth, primarily reflecting differences in the thermal lake regime (e.g. Choi 1998) (Fig. 1a). The effects of lake productivity on fish size did not show a consistent trend although for many species a decrease in average size with increasing concentration of total phosphorus (TP) was observed (Jeppesen *et al.* 2000, 2010) (Fig. 1a). The response of maximum size along geographical (and thermal) gradients is apparently species-specific and not unidirectional (Belk & Houston 2002; Blanck & Lamouroux 2007) (Fig. 1b). An increase in lake area and depth and a decrease in the intensity of anthropogenic modifications in the lakes' catchment is predicted to result in larger average fish sizes and larger maximum-sized individuals due to lower anthropogenic disturbances such as fishing (Wilde & Pope 2004) (Fig. 1b). We predicted a flattening of the ISD slope (i.e. less negative) with increasing latitude, elevation, lake area and lake depth, and in pristine lakes of low productivity due to higher proportions of large fish (*cf*. Emmrich *et al.* 2011). Finally, an increase in lake productivity should lead to an increase in small-sized fish, which in turn steepens the slope of the ISD (Fig. 1c). Overall, we expected a high biogeographic heterogeneity of the size structures of lake fish assemblages, due to the varying strength, direction and the potentially interacting effects of local abiotic predictors on fish size.

Methods

Fish data

A database of multi-mesh gillnet catches was used to analyse differences in the size structure of European lake fish assemblages. Natural lakes and reservoirs (both termed lakes subsequently) were sampled between 1993 and 2010, largely in accordance with the European standard EN14757 for gillnet surveys in lakes (CEN (European Committee for Standardization) 2005). Stratified random sampling with benthic multi-mesh gillnets (type NORDIC: length 30 m; height 1.5 m; 12 panels of 2.5 m each with mesh sizes between 5 and 55 mm knot to knot) was undertaken during late summer and early autumn with a pre-defined number of nets per lake set randomly in each depth stratum depending on lake area and depth.

Information on individual size is essential for a representative picture of fish assemblage size structure and for the calculation of size metrics. We selected only lakes with available information on individual length (nearest cm) and/or fresh mass (nearest g) for at least 95% of the fish. Missing size measures were back-calculated using latitudinal-specific (5° latitude) and species-specific mass-length and length-mass relationships calculated from fish in the database with complete information on individual length and fresh mass (Emmrich unpublished). Due to biased sampling efficiency of multi-mesh gillnets for very small fish (Prchalová *et al.* 2009), individuals < 8 cm were ignored in order to reduce the 'noise' of varying seasonal recruitment success and differences in sampling time and, hence, the length of effective growing season. Only lakes sampled with a minimum of six gillnets and with a catch size of ≥ 50 individuals were considered to ensure that size metrics were not heavily influenced by highly variable catches of single nets and by extreme sizes within small sample sizes. Finally, only lakes with pH ≥ 6 were included which avoids interfering effects of acidification on the fish assemblage size structure. The final dataset comprised fish catch data from 701 lakes (615 natural lakes and 86 reservoirs) located in eight European countries (Fig. 2).

Predictor variables

Nine predictor variables were selected for this study (Table 1). Lake location was characterised using latitudinal coordinates (map datum WGS84) and elevation (m a.s.l.). Lake morphometry was characterised by area (km^2) and maximum depth (m). Trophic status was characterised using annual mean total phosphorus concentration (TP in $\mu g\ L^{-1}$). The catchment area of the lakes was described by the percentage of natural ground (Corine Land Cover ($CLC_{natural}$), European Environment Agency 2006) indicating the proportion of area which is not affected by anthropogenic alterations such as agriculture or urbanisation.

Fish assemblage composition was described using local species numbers (richness). Furthermore, we conducted a principle component analysis (PCA) derived with a Chord-transformed site-species matrix including numerical abundance data. This unconstrained ordination allows the application of Euclidean distance-based PCA on zero-inflated datasets (Legendre & Gallagher 2001). Zero-inflated data are typically observed when many species are replaced across broad gradients of abiotic lake characteristics (area, depth, trophic status) and geographic position (Table 1). The Chord distance downweighs the importance of rare species (Legendre & Gallagher 2001) which was important as highly abundant species were also most influential for the calculation of the size metrics. To reduce further the number of zeros in the site-species matrix, rare species which have been caught in less than five lakes (<1% of 701 lakes) were removed from the analyses. The site (lake) scores along the first two PCA axes were used as taxonomic descriptors of the lake fish assemblages.

Size metrics

To cover different aspects of the size structure of lake fish assemblages, we selected four size metrics. We calculated the average size (AS) as the geometric mean length (cm) of the fish per lake and the maximum size (S_{max}, cm) as the length of the largest individual in the catch. The relative frequency of small and large fish in a lake was characterised by the individual size distribution (ISD) (*sensu* size spectra, White *et al.* 2007). ISDs represent a frequency distribution of individual body sizes across size classes irrespective of taxonomy (White *et al.* 2007). ISDs typically follow simple power laws (Kerr & Dickie 2001) which are characterised by monotonically decreasing, unimodal and multimodal distributions (White *et al.* 2007). Size groups were based on $\log_2$ class intervals of fresh mass (g). Due to the removal of fish < 8 cm, the smallest individuals of 1-8 g were summed in the first fresh mass class, and all fish > 4096 g were summed in the last (11^{th}) fresh mass class. Because ISDs were based on log-size classes, assumptions of multiplicative log-normal error structures were better supported than additive normal error structures. Consequently, log-linear ordinary least square (OLS) regressions were calculated (Xiao *et al.* 2011) by plotting the midpoint of each $\log_2$ fresh mass class against the $\log_2$-transformed number of individuals per size class. To improve between-lake comparability, regression slopes from the log-linear models were initially calculated as a size metric for all lakes, independently of whether nonlinear models would have been better fit. To account for deviations from log-linear models, the determination coefficient (R^2) of the regression lines was additionally considered as a size metric in the subsequent analyses. In the case of non-significant log-linear models, we explored whether data were alternatively better described by unimodal or multimodal models.

Data analyses

Variations in the size metrics were modelled along gradients of abiotic lake characteristics and differences in fish assemblage composition using boosted regression tree (BRT) analysis. BRT analysis is a predictive technique which combines boosting algorithms with regression trees, and considers nonlinear response-predictor relationships as well as interactions between predictors (Friedman 2002; De'ath 2007). BRTs were applied to estimate the contribution of each predictor to the total variation in each of the four size metrics. Interactions between predictors were automatically included in the models via tree complexity. Similar to other tree-based methods, BRTs can simultaneously handle categorical and continuous data, and allow the incorporation of missing data. Predictor variables do not need to be transformed and outliers need not to be eliminated (Breiman *et al.* 1984; De'ath 2007). A Gaussian error distribution was most appropriate for the size metrics. Predictive performance of the BRT models was evaluated using ten-fold cross-validation. Ten mutually exclusive data subsets were randomly selected and model predictions were compared to the withhold proportion of the data. The optimal number of trees (nt) which produced the lowest prediction error without model overfitting was identified testing tree complexities (tc) of one and two (this accounts for no or one-way interactions), learning rates (lr) of 0.05, 0.01, 0.005 and 0.001 and bag fractions (bf) of 0.5 and 0.75. The bag fraction determines the proportion of data which are selected during each iteration process. The bag fraction introduces stochasticity, improves model accuracy and reduces model overfitting (Friedman 2002). The minimum limit to fit models was set to 1000 trees to reduce the contribution from single trees to the final model (Elith, Leathwick, & Hastie 2008). BRT analysis does not generate P-values, but the relative influence (measuring how often a predictor variable is selected and testing the strength of its influence on model improvement) was used to estimate the significance of each predictor. Partial dependence plots were used to visualize the effects of individual predictors on the response variables (size metrics) after accounting for the average effects of all other predictors (Friedman 2002).

Complete information on TP and $CLC_{natural}$ was available for 51.5% and 47.9% of the lakes, respectively, but this is not a problem in BRT analysis as dummy values replace missing entries. To evaluate whether the dummy values changed the relative influence of predictor variables, the models were re-run with a reduced lake set (n=274), comparable in geographical range to the total dataset, with complete information on TP and $CLC_{natural}$ (Table S2 supporting information). Statistical analyses were performed in R (R Development Core Team 2012) version 2.14.2 using the packages vegan (version 2.0-3; Oksanen *et al.* 2012) for PCA calculation and gbm (version 1.6-3.2; Ridgeway 2012) plus codes provided by Elith *et al.* (2008) for calculation of the BRT models. Published R codes from Xiao *et al.* (2011) were used to test the error structure of the ISD data.

Results

Fish assemblage composition

A total of 37 fish species was caught in the benthic multi-mesh gillnets in 701 European lakes. Perch *Perca fluviatilis* L. and roach *Rutilus rutilus* (L.) dominated the overall catch (Table S1 supporting information). The first two PCA axes explained 67.9% of the variability in fish assemblage composition (axis 1: 43.4%; axis 2: 24.5%). Further axes were less important (< 9% explained variability). Axis 1 discriminated perch-dominated lakes (Pearson's r = -0.87) from roach-dominated lakes (r = 0.80). Roach-dominated lakes were characterised by higher abundances of bream (*Abramis brama* (L.), r = 0.36) and white bream (*Blicca bjoerkna* (L.), r = 0.32). The positive lake scores along axis 1 represent fish assemblages dominated by eurythermic warmwater cyprinids, and the negative lake scores along axis 1 represent fish assemblages dominated by eurythermic coolwater perch. Axis 2 discriminated salmonid-dominated lakes with stenothermic coldwater species such as brown trout (*Salmo trutta* L., r = -0.78) and charr (*Salvelinus* ssp., r = -0.53) from lakes dominated by eurythermic roach (r = 0.59) and perch (r = 0.48). Other species were less important in the ordination (all r < 0.3, Table S1 supporting information).

Size metrics

Average size (AS) of the fish assemblages was 14.1 ± 2.6 cm (SD). Mean S_{max} was 54.6 ± 15.4 cm (SD). Fish catches from most lakes (n = 633) could be characterised by significantly linear ($p < 0.05$) ISDs which indicate a monotonically decreasing pattern (Fig. 3a). The slopes of the OLS regression lines of these 633 lakes averaged -0.74 (95% CI = -0.75 – -0.72; range -1.24 – -0.31). Mean R^2 of the regression models was 0.78 ± 0.15 (SD). Size structures of lake fish assemblages characterised by non-significant linear ISDs fitted quadratic models which represent unimodal (n = 51, Fig. 3b) and multimodal ISDs. Multimodal ISDs were typically shaped by two peaks (n = 17, Fig. 3c). The range of the size metrics was substantial, but the most extreme values occurred in only a few lakes (Fig. 4 a-d). The majority of the lakes were characterised by a relatively similar AS, slope and R^2 of the ISD which was indicated by a steep increase in the cumulative percentages around the modal values (Fig. 4 a,c,d). The distribution of S_{max} was more heterogeneous with most maximum-sized fish lengths between 35 and 75 cm (Fig. 4b).

BRT models

Final BRT models were run with learning rates of 0.01 (ISD, R^2) and 0.005 (AS, S_{max}), a bag fraction of 0.75 and a tree complexity of two (i.e. one-way interactions between the predictors were included). Optimal tree number ranged between 1250 and 2850. Predictive model performance was 36.1%

(AS), 22.7% (S_{max}), 46.7% (slope ISD) and 42.5% (R^2). The BRT models developed with data from the reduced lake set (n = 274 with complete information of TP and $CLC_{natural}$) resulted in comparable predictive model performances, and the importance and rank of predictors did not change substantially. This suggests that the missing data on trophic status and $CLC_{natural}$ had no substantial effect on the dominant predictors which influence fish assemblage size structure in our data set (Table S2 supporting information).

Predictor influence and interactions between predictors

Relative influence (RI) of the predictors differed among the size metrics (Table 2). The functions fitted to the BRT models were highly variable and revealed linear and curvilinear patterns (Fig. 5). RI of TP and $CLC_{natural}$ was consistently weak across the size metrics (RI < 5%) (Table 2). The other predictors contributed stronger to variations in the size metrics (RI > 8%), and elevation, latitude, lake area, species richness and scores to PCA axis 2 were ranked highest (Table 2).

The largest AS was observed in fish assemblages populating southern and northern European lakes. These lakes were located at higher elevation, and fish assemblages were dominated by salmonids (mainly brown trout and/or charr) (Figs 5a and 6a). The smallest AS was observed in European lowland lakes with fish assemblages dominated by perch and/or roach (Figs 5a and 6a). The largest S_{max} was observed in the largest lakes populated by many species. Fish assemblages in these lakes were typically dominated by warmwater cyprinids (Figs 5b and 6b). The slope of the ISDs decreased (i.e. became less negative) with increasing elevation. Smaller lakes with low species richness and lakes with fish assemblages dominated by salmonids were characterised by the flattest slopes (Figs 5c and 6c) and the lowest R^2 which indicates nonlinear ISDs (Figs 5d and 6d).

Discussion

Results from the BRT analysis of the four size metrics revealed elevation, latitude and lake area as important abiotic predictors of the size structure of European lake fish assemblages. These results support our initial predictions obtained from regional analyses which have confirmed a strong effect of geographical location via the local temperature. Surprisingly and in contrast to our predictions, lake productivity had the weakest influence on differences in the size structure of lake fish assemblages when analysed over large geographical scales. Fundamentally new insights emerged from the inclusion of biotic descriptors. Species shifts across the long elevation and latitudinal gradients generated two fish assemblage types which strongly differed in their size structure. More than 90% of the lakes, primarily located in the European lowlands, were characterised by fish assemblages which were dominated by small-sized perch and/or roach. The fish assemblages of

about 10% of the lakes mainly located at higher elevation in southern and northern Europe were dominated by salmonids (brown trout and/or charr). These assemblages were characterised by a significantly lower proportion of small-sized fish which, in turn, resulted in a higher average size of the assemblages characterised by unimodal or multimodal ISDs.

Elevation and latitude which can be linked to the environmental temperature and the thermal lake regime (Efremova & Palshin 2007) were important predictors of AS, and the slope and R^2 of the ISDs. Temperature has a significant effect on the size of aquatic ectotherms from individual to assemblage levels (Daufresne, Lengfellner & Sommer 2009), and strongly modifies species richness and taxonomic composition of lake fish assemblages (Tammi *et al.* 2003; Jeppesen *et al.* 2012). We observed more large fish in colder environments. This pattern supports the temperature-size rule (Atkinson 1994) which describes the phenotypically plastic response of body size of ectothermic species to their environmental temperature. Individuals in colder environments grow slower early in ontogeny and mature as larger adults than individuals in warm environments. Thus, individual body size of fish decreases with increasing temperature (Daufresne *et al.* 2009).

Maximum fish length was the only size metric whose variation was not primarily linked to elevation and latitude. The BRT model of maximum length had a substantially lower predicted performance in the boosted regressions than the other size metrics. Other empirical studies on freshwater fish have confirmed comparable weak shifts of maximum fish size along geographic gradients (Belk & Houston 2002; Blanck & Lamouroux 2007). Instead, we identified lake area as the main predictor of maximum fish length, likely because the largest individuals are less vulnerable to fisheries in large lakes (Wilde & Pope 2004). Furthermore, food-chain length in lakes is primarily determined by lake size (Post *et al.* 2000), and larger lakes support more trophic levels and are consequently populated with larger top predators. A similar pattern was suggested from a regional study studying maximum fish size in European lowland lakes (Emmrich *et al*. 2011). Finally, maximum length was positively correlated with species richness which indicates a higher probability of occurrence and catch of large-sized species in large lakes.

Although the lakes in this study covered a productivity gradient from ultra-oligotrophic to hypertrophic, and lake catchments strongly differed in the proportion of area which was anthropogenically modified (agriculture, urbanisation), both predictors did not significantly explain variability in the size structure of lake fish assemblages. Trophic status and lake temperature are closely linked via lake depth. Shallow (warm) lakes are typically nutrient rich (Nõges 2009) and fish densities increase in number and biomass with increasing lake productivity (Jeppesen *et al.* 1997). At comparable or even reduced nutrient concentrations warmwater lakes exhibit higher fish densities

particularly of small-sized individuals than coldwater lakes (Jeppesen *et al.* 2010). Fish in warmwater lakes which are characterised by relatively instable thermal regimes grow faster early in ontogeny, but slower later in ontogeny, mature earlier and have shorter life spans than fish in coldwater lakes with more stable thermal regimes (Choi 1998; Blanck & Lamouroux 2007; Jeppesen *et al.* 2010). This explains another dimension of the key influence of temperature on the size structure of lake fish assemblages when compared across large geographical and climatic gradients. The interaction between lake morphometry, temperature and productivity might explain why trophic status, contrary to our initial predictions, was such a poor predictor in our study. Presumably, effects of variation in trophic status were covered by temperature variations which affect size structure in the same direction.

A surprisingly high homogeneity of the fish assemblage size structure was apparent in 90% of the lakes which were mainly located in the European lowlands (Northern Germany, Southern Sweden). Relatively small fish dominated the size-frequency distributions in these lakes. This dominance of small-sized individuals can be due to the occurrence of many small-sized species and/or due to high abundances of juvenile fish (Teixeira-de Mello *et al.* 2009; Daufresne *et al.* 2009). Small-sized species typically inhabit the shallow near-shore lake zones and tend to be underestimated in benthic multi-mesh gillnet catches (Diekmann *et al.* 2005). Consequently, we assume that the dominance of small fish sizes in our study lakes primarily reflects high juvenile abundances. In the European lowlands, local temperature defined by lake depth and latitude determines fish species composition and relative species abundance (Mehner *et al*. 2005; 2007). Specifically, fish assemblages of these lakes are typically dominated by perch and/or roach (Mehner *et al.* 2005; 2007). This assemblage pattern was well described by the first PCA axis on fish assemblage composition, which discriminated perch-dominated lakes from roach-dominated lakes. However, the lakes scores of PCA axis 1 did not predict variability of any size metric. The weak relative influence of this biotic predictor may be explained by similar size structures of perch and roach populations in the dataset (mean total length perch: 14.1 cm; roach: 14.5 cm). The size distribution of both species was not significantly different (two sample Kolmogorov-Smirnov test: $D = 0.16$, $P = 0.62$). The small average size and the steep ISD slopes indicated that juvenile fish dominated these assemblages.

The overall size structure of lowland lake fish assemblages is apparently relatively invariant and largely species-independent, due to similar life histories of locally dominant species. This conclusion does not contrast with results from earlier studies in this region, in which a correspondence between the size structures of fish populations and multi-species assemblages with gradients of lake morphometry and trophic status has been documented (Jeppesen *et al.* 2000; Holmgren & Appelberg 2000; Emmrich *et al.* 2011). However, the subtle response of fish size to local predictors in

these regional studies is relativised when shifts in lake fish assemblage size structure are considered across large geographical scales.

The size structure of fish assemblages in lowland lakes which were dominated by roach and/or perch differed essentially from lakes populated by stenothermic coldwater species such as brown trout and/or charr. These salmonid species occurred primarily in high elevation lakes but at both the northern and southern latitudinal range, suggesting that the colder temperature at higher elevation was the main factor determining their occurrence. The trout and charr populations were characterised by similar size structures (two sample Kolmogorov Smirnov Test: $D = 0.14$, $P = 0.64$), and were dominated by larger-sized fish resulting in unimodal and bimodal size distributions, and lower abundances of small-sized juvenile individuals (*cf*. L'Abée-Lund, Langeland, & Sægrov 1992; Griffiths 1994).

The major shift in the size structure of European lake fish assemblages with increasing elevation and decreasing temperature reflects a switch in the dominant life-history strategy. Cyprinids and percids (mainly perch) are characterised by early maturity, lower fecundity and smaller adult size, and are classified as species with a life-history strategy of the periodic type (Vila-Gispert & Moreno-Amich 2002). A periodic life history enables survival during suboptimal environmental conditions in the northern hemisphere such as reduced food availability during winter (Winemiller & Rose 1992). The size structure of fish assemblages dominated by the periodic life-history type is characterised by a dominance of small-sized, juvenile fish. By contrast, larger-sized salmonids are species that mature later, have higher fecundity and larger sizes. Salmonids are typically classified as species with a life-history strategy of the equilibrium type (Winemiller & Rose 1992). Their size structure is dominated by more medium- and large-sized fish and lower abundances of juveniles. We cannot exclude the possibility that abundances of small fish are underestimated due to the low catchability of juvenile salmonids by multi-mesh gillnets (Finstad et al. 2000). The low abundance of small-sized juveniles in some of these lakes may also reflect the occupancy of habitats other than lakes such as adjacent rivers. Despite these methodological uncertainties, there is strong evidence for a switch from a cyprinid-like life history to a salmonid-like life history along the elevation gradient in European lakes. This shift has substantial consequences for the overall size structure of the lake fish assemblages.

Our results suggest a strong temperature effect on the dominant life-history type in lake fish assemblages. Specifically, life history strategies of roach and perch which are dominant in European lowland lakes are likely to be not plastic enough for a successful recruitment at coldest temperatures in higher elevation lakes. These species are then replaced by salmonids which are better adapted to cold environments (*cf.* Helland *et al.* 2011). In turn, salmonids can obviously not develop a more

periodic life history strategy similar to that found in perch and roach, and hence fail to become dominant in shallower and warmer lakes at low elevation sites.

We found evidence that changes in the size structure of lake fish assemblages across broad geographical ranges consist of size shifts at both population (intraspecific) and assemblage (interspecific) levels. These two response levels have to be cautiously disentangled when the effects of temperature-related predictors on size structure of assemblages has to be discussed.

In summary, many of our predictions of environmental determinants on the size structure of European lake fish assemblages were supported. Average fish size increased with increasing elevation and latitude and larger maximum-sized fish populated large lakes. Contrary to our assumptions, lake productivity had no significant influence when compared across a large geographical scale. The two major species shifts differed in their consequences. Shifts from roach to perch dominance in European lowland lakes resulted in low variation in the size structure. The shift from perch and/or roach to salmonids with increasing elevation induced a strong shift towards larger-sized fish in salmonid-dominated assemblages. This suggests that size structures of fish assemblages in European lowland lakes are relatively robust against environmental modifications. In contrast, fish assemblages of high-elevation lakes likely suffer dramatic changes, in consequence of global warming, for instance (Jeppesen *et al.* 2012). Expected species shifts are likely to be accompanied by substantial shifts in size structure with unprecedented effects on species interactions and energy flows in lake ecosystems (*cf*. Dossena *et al.* 2012).

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Literature

Arend, K.K. & Bain, M.B. (2008) Fish communities in coastal freshwater ecosystems: the role of the physical and chemical setting. *BMC Ecology*, **8**, 23.

Atkinson, D. (1994) Temperature and organism size - a biological law for ectotherms? *Advances in Ecological Research*, **25**, 1–58.

Atkinson, D. & Sibly, R.M. (1997) Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends in Ecology & Evolution*, **12**, 235–239.

Beier, U. (2001) Habitat distribution and size structure in freshwater fish communities: effects of vendace on interactions between perch and roach. *Journal of Fish Biology*, **59**, 1437–1454.

Belk, M.C. & Houston, D.D. (2002) Bergmann's rule in ectotherms: A test using freshwater fishes. *American Naturalist*, **160**, 803–808.

Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., Manickchand-Heileman, S., Paya, I., Sainsbury, K., Sanchez, F. & Zwanenburg, K. (2000) Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science*, **57**, 558–571.

Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McCloghrie, P., Rochet, M.J. & Benoit, E. (2009) How does abundance scale with body size in coupled size-structured food webs? *Journal of Animal Ecology*, **78**, 270–280.

Blanck, A. & Lamouroux, N. (2007) Large-scale intraspecific variation in life-history traits of European freshwater fish. *Journal of Biogeography*, **34**, 862–875.

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R. & Sams, S. (1978) Relationships between body size and some life history parameters. *Oecologia*, **37**, 257–272.

Breimann, L., Friedman, J.H., Olshen, R.A. & Stond, C.J. (1984) Classification and regression trees. Wadsworth International Group, Belmont.

Calder, W.A. (1984) Size function and life history. Harvard University Press, Cambridge.

CEN, (2005) Water quality – Sampling of fish with multi-mesh gillnets. European Committee for Standardization. Ref. No. EN 14757:2005.

Choi, J.S. (1998) Lake ecosystem responses to rapid climate change. *Environmental Monitoring and Assessment*, **49**, 281–290.

Daufresne, M., Lengfellner, K. & Sommer, U. (2009) Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*, **106**, 12788–12793.

De'ath, G. (2007) Boosted trees for ecological modeling and prediction. *Ecology*, **88**, 243–251.

Diekmann, M., Brämick, U., Lemcke, R. & Mehner, T. (2005) Habitat-specific fishing revealed distinct indicator species in German lowland lake fish communities. *Journal of Applied Ecology*, **42**, 901–909.

Dossena, M., Yvon-Durocher, G., Grey, J., Montoya, J.M., Perkins, D.M., Trimmer, M. & Woodward, G. (2012) Warming alters community size structure and ecosystem functioning. *Proceedings of the Royal Society B: Biological Sciences*, in press, doi: 10.1098/rspb.2012.0394

Efremova, T. & Palshin, N. (2007) Effect of climate and morphometry on thermal regime of lakes. 16th International Northern Research Basins Symposium and Workshop Petrozavodsk, Russia 36–44.

Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802–813.

Elton, C. (1927) Animal ecology. Macmillan, New York.

Emmerson, M.C. & Raffaelli, D. (2004) Predator-prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, **73**, 399–409.

Emmrich, M., Brucet, S., Ritterbusch, D. & Mehner, T. (2011) Size spectra of lake fish assemblages: responses along gradients of general environmental factors and intensity of lake-use. *Freshwater Biology*, **56**, 2316–2333.

European Environment Agency (2006) Corine Land Cover 2006 raster data. Available at: http://www.eaa.europe.eu.

Finstad, A.G., Jansen, P.A. & Langeland, A. (2000) Gillnet selectivity and size and age structure of an alpine Arctic char (*Salvelinus alpinus*) population. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1718-1727.

Friedman, J.H. (2002) Stochastic gradient boosting. *Computational Statistics & Data Analysis*, **38**, 367–378.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. & Heinsohn, R. (2011) Declining body size: a third universal response to warming? *Trends in Ecology & Evolution*, **26**, 285–291.

Griffiths, D. (1994) The size structure of lacustrine Arctic charr (Pisces: Salmonidae) populations. *Biological Journal of the Linnean Society*, **51**, 337–357.

Griffiths, D. (2006) Pattern and process in the ecological biogeography of European freshwater fish. *Journal of Animal Ecology*, **75**, 734–751.

Griffiths, D. (2010) Pattern and process in the distribution of North American freshwater fish. *Biological Journal of the Linnean Society*, **100**, 46–61.

Heibo, E., Magnhagen, C. & Vøllestad, L.A. (2005) Latitudinal variation in life-history traits in Eurasian perch. *Ecology*, **86**, 3377–3386.

Helland, I.P., Finstad, A.G., Forseth, T., Hesthagen, T. & Ugedal O. (2011): Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology*, **80**, 539-547.

Holmgren, K. & Appelberg, M. (2000) Size structure of benthic freshwater fish communities in relation to environmental gradients. *Journal of Fish Biology*, **57**, 1312–1330.

Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T. & Landkildehus, F. (2000) Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwater Biology*, **45**, 201–218.

Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., Pedersen, L.J. & Jensen, L. (1997) Top-down control in freshwater lakes: The role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia*, **342**, 151–164.

Jeppesen, E., Meerhoff, M., Holmgren, K., Gonzalez-Bergonzoni, I., Teixeira-de Mello, F., Declerck, S.A.J., De Meester, L., Søndergaard, M., Lauridsen, T.L., Bjerring, R., Conde-Porcuna, J.M., Mazzeo, N., Iglesias, C., Reizenstein, M., Malmquist, H.J., Liu, Z.W., Balayla, D. & Lazzaro, X. (2010) Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. *Hydrobiologia*, **646**, 73–90.

Jeppesen, E., Mehner, T., Winfield, I., Kangur, K., Sarvala, J., Gerdeaux, D., Rask, M., Malmquist, H., Holmgren, K., Volta, P., Romo, S., Eckmann, R., Sandström, A., Blanco, S., Kangur, A., Ragnarsson Stabo, H., Tarvainen, M., Ventelä, A.-M., Søndergaard, M., Lauridsen, T. & Meerhoff, M. (2012) Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *Hydrobiologia*, **694**, 1-39.

Kerr, S.R. & Dickie, L.M. (2001) The biomass spectrum: A predator-prey theory of aquatic production. Columbia University Press, New York.

Knouft, J.H. (2004) Latitudinal variation in the shape of the species body size distribution: an analysis using freshwater fishes. *Oecologia*, **139**, 408–417.

L'Abée-Lund, J.H., Langeland, A. & Sægrov, H. (1992) Piscivory by brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.) in Norwegian lakes. *Journal of Fish Biology*, **41**, 91–101.

Lappalainen, J., Tarkan, A.S. & Harrod, C. (2008) A meta-analysis of latitudinal variations in life-history traits of roach, *Rutilus rutilus*, over its geographical range: linear or non-linear relationships? *Freshwater Biology*, **53**, 1491–1501.

Legendre, P. & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.

Lindsey, C.C. (1966) Body sizes of poikilotherm vertebrates at different latitudes. *Evolution*, **20**, 456–465.

Mehner, T., Diekmann, M., Brämick, U. & Lemcke, R. (2005) Composition of fish communities in German lakes as related to lake morphology, trophic state, shore structure and human-use intensity. *Freshwater Biology*, **50**, 70–85.

Mehner, T., Holmgren, K., Lauridsen, T.L., Jeppesen, E. & Diekmann, M. (2007) Lake depth and geographical position modify lake fish assemblages of the European 'Central Plains' ecoregion. *Freshwater Biology*, **52**, 2285–2297.

Nõges, T. (2009) Relationships between morphometry, geographic location and water quality parameters of European lakes. *Hydrobiologia*, **633**, 33–43.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P.M., Stevens, H.H. & Wagner H. (2012) vegan: Community ecology package. R package version 2.0-3.

Petchey, O.L. & Belgrano, A. (2010) Body-size distributions and size-spectra: universal indicators of ecological status? *Biology Letters*, **6**, 434–437.

Peters, R.H. (1983) The ecological implication of body size. Cambridge University Press, Cambridge.

Post, D.M., Pace, M.L. & Hairston, N.G. (2000) Ecosystem size determines food-chain length in lakes. *Nature*, **405**, 1047–1049.

Prchalová, M., Kubečka, J., Říha, M., Mrkvička, T., Vašek, M., Jůza, T., Kratochvíl, M., Peterka, J., Draštík, V. & Křížek, J. (2009) Size selectivity of standardized multimesh gillnets in sampling coarse European species. *Fisheries Research*, **96**, 51–57.

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org.

Ridgeway G. (2012) gbm: Generalized boosted regression models. R package version 1.6-3.2.

Reuman, D.C. & Cohen, J.E. (2005) Estimating relative energy fluxes using the food web, species abundance, and body size. *Advances in Ecological Research*, **36**, 137–182.

Tammi, J., Appelberg, M., Beier, U., Hesthagen, T., Lappalainen, A. & Rask, M. (2003) Fish status survey of Nordic lakes: Effects of acidification, eutrophication and stocking activity on present fish species composition. *Ambio*, **32**, 98–105.

Teixeira-de Mello, F., Meerhoff, M., Pekcan-Hekim, Z. & Jeppesen, E. (2009) Substantial differences in littoral fish community structure and dynamics in subtropical and temperate shallow lakes. *Freshwater Biology*, **54**, 1202–1215.

Vila-Gispert, A. & Moreno-Amich, R. (2002) Life-history patterns of 25 species from European freshwater fish communities. *Environmental Biology of Fishes*, **65**, 387–400.

White, E.P., Ernest, S.K.M., Kerkhoff, A.J. & Enquist, B.J. (2007) Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution*, **22**, 323–330.

Wilde, G.R. & Pope, K.L. (2004) Relationship between lake-record weights of fishes and reservoir area and growing season. *North American Journal of Fisheries Management*, **24**, 1025–1030.

Winemiller, K.O. & Rose, K.A. (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2196–2218.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. & Warren, P.H. (2005) Body size in ecological networks. *Trends in Ecology & Evolution*, **20**, 402–409.

Xiao, X., White, E.P., Hooten, M.B. & Durham, S.L. (2011) On the use of log-transformation vs. nonlinear regression for analyzing biological power laws. *Ecology*, **92**, 1887–94.

Yvon-Durocher, G., Reiss, J., Blanchard, J., Ebenman, B., Perkins, D.M., Reuman, D.C., Thierry, A., Woodward, G. & Petchey, O.L. (2011) Across ecosystem comparisons of size structure: methods, approaches and prospects. *Oikos*, **120**, 550–563.

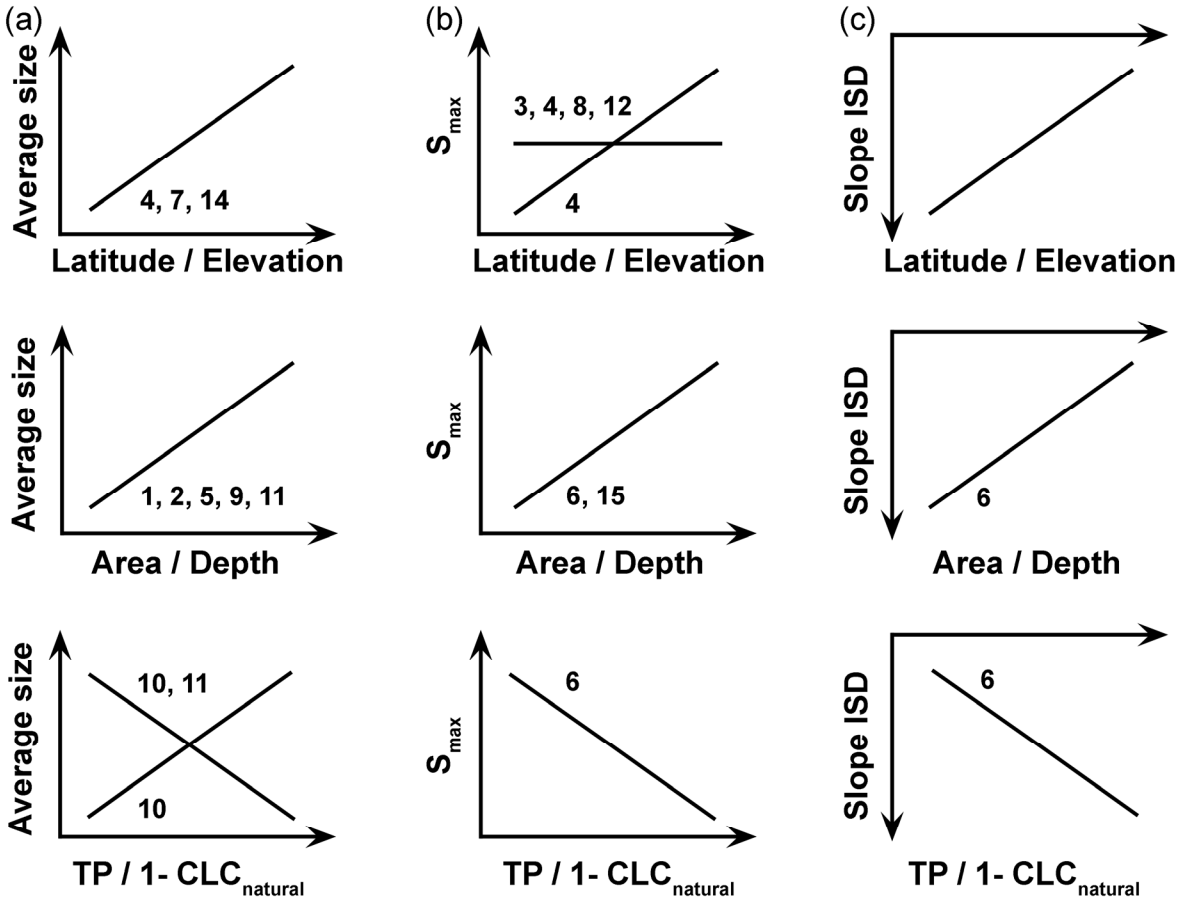

Figure 1. Predicted trends in average size (a), maximum size (S_{max}) (b) and the slope of the individual size distribution (ISD) (c) along gradients of descriptors related to the lakes' location, morphometry, trophic status and anthropogenic impact in the catchment area (measured as Corine Land Cover; $CLC_{natural}$). Lines show a decreasing, increasing or indeterminate (horizontal line) response of the size metrics. Note the opposite direction of the ordinate, because of the negative slopes of the ISD (c). Numbers indicate empirical studies supporting the predictions:

1: Arend & Bain (2008), 2: Beier (2001), 3: Belk & Houston (2002), 4: Blanck & Lamouroux (2007), 5: Choi (1998), 6: Emmrich *et al.* (2011), 7: Griffiths (2006), 8: Heibo *et al.* (2005), 9: Holmgren & Appelberg (2000), 10/11: Jeppesen *et al.* (2000, 2010), 12: Lappalainen *et al.* (2008), 13: Lindsey (1966), 14: Teixeira-de Mello *et al.* (2009), 15: Wilde & Pope (2004)

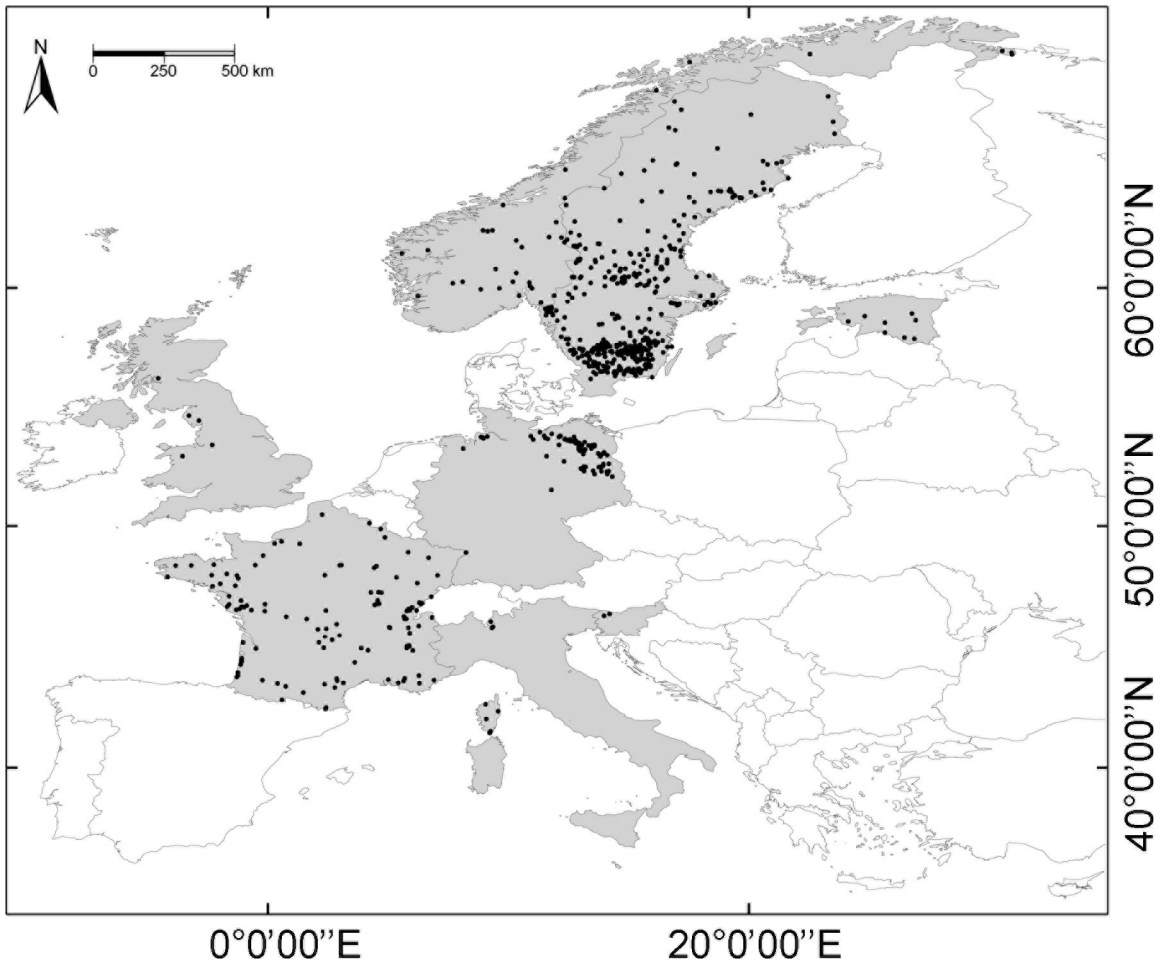

Figure 2. Geographical distribution of the 701 lakes across eight European countries (grey-coloured) whose fish assemblages were sampled with benthic multi-mesh gillnets.

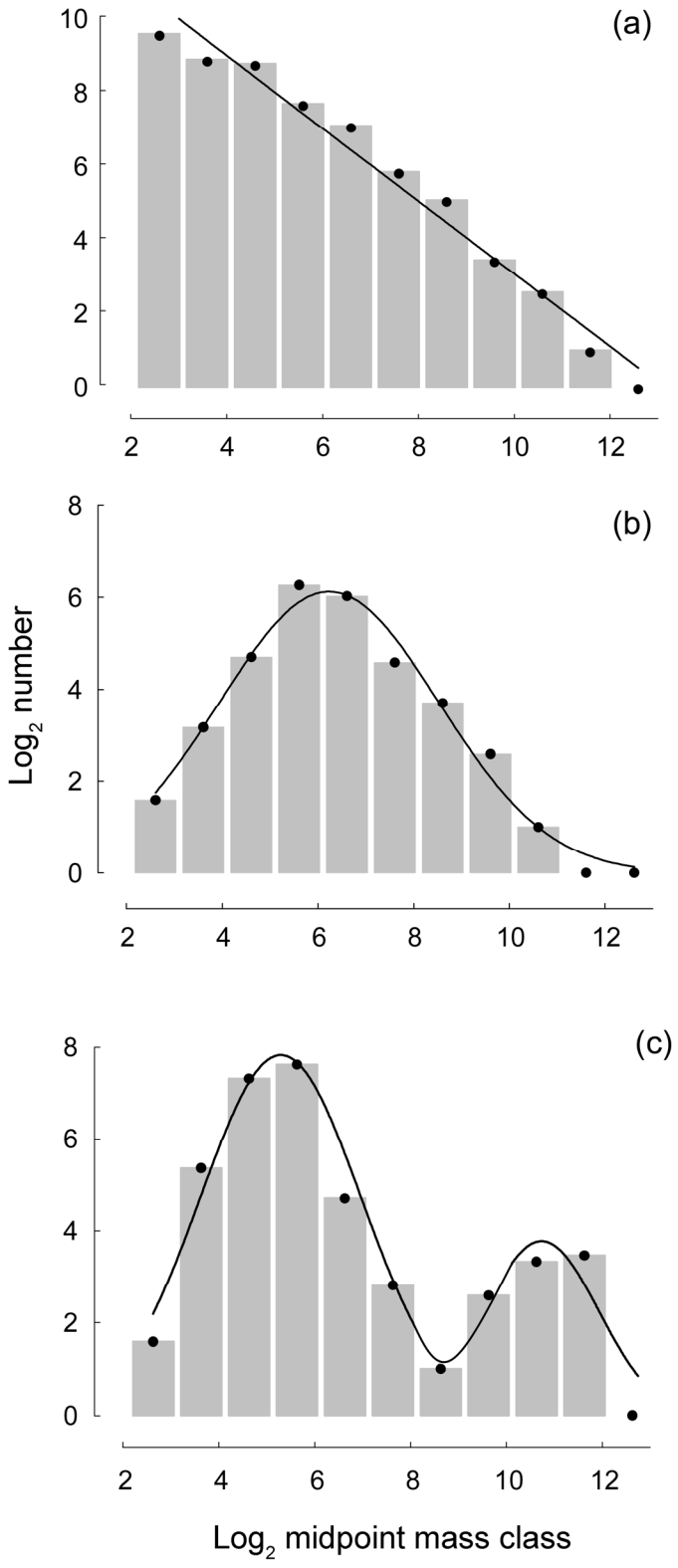

Figure 3. Examples of individual size distributions (log_2 midpoints of fresh mass in g vs. log_2 numbers) of fish assemblages from three European lakes showing a monotonically decreasing (a), an unimodal (b) and a multimodal distribution (c).

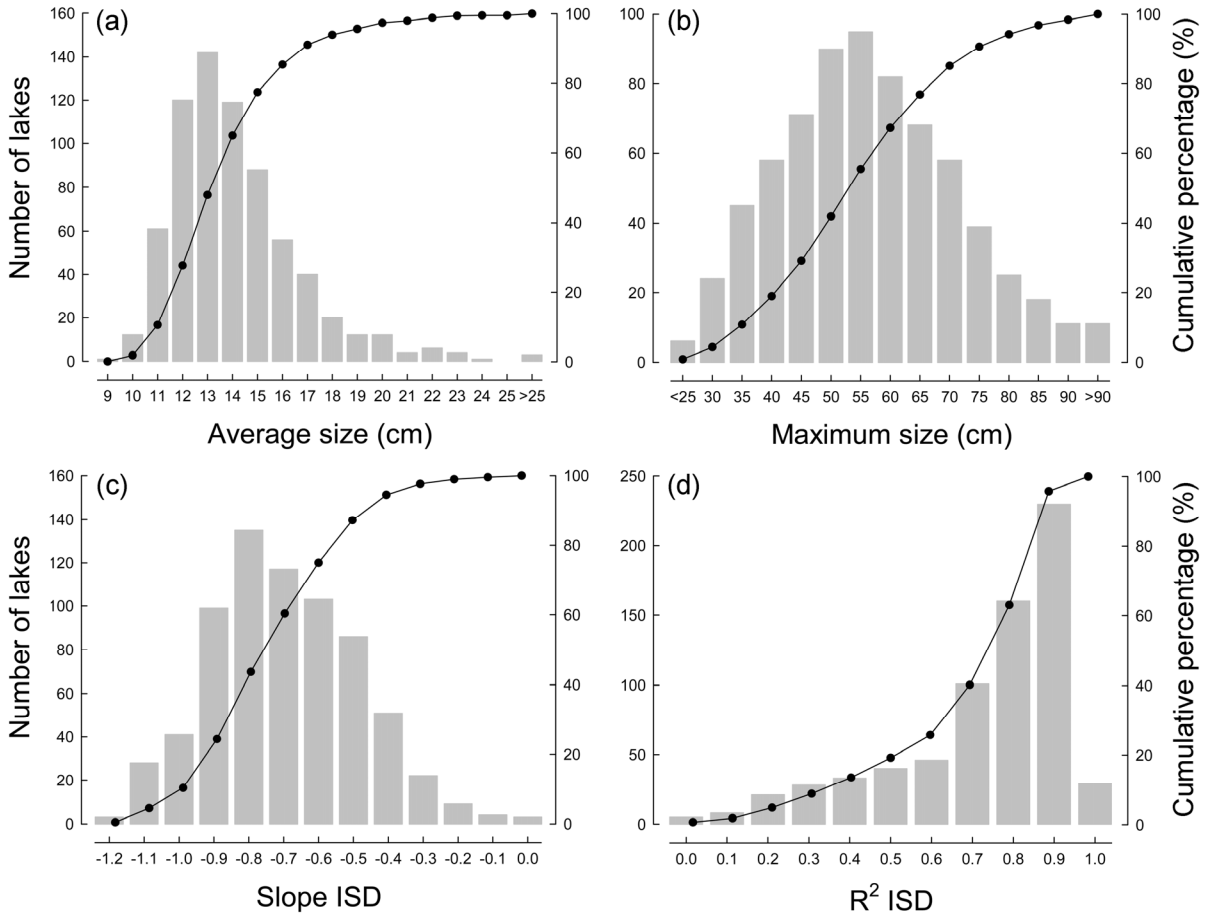

Figure 4. Frequency distribution of average size (a), maximum size (b) and the slope (c) and R^2 (d) of the individual size distributions (ISD). The black lines indicate the cumulative distribution of the size metrics in percent.

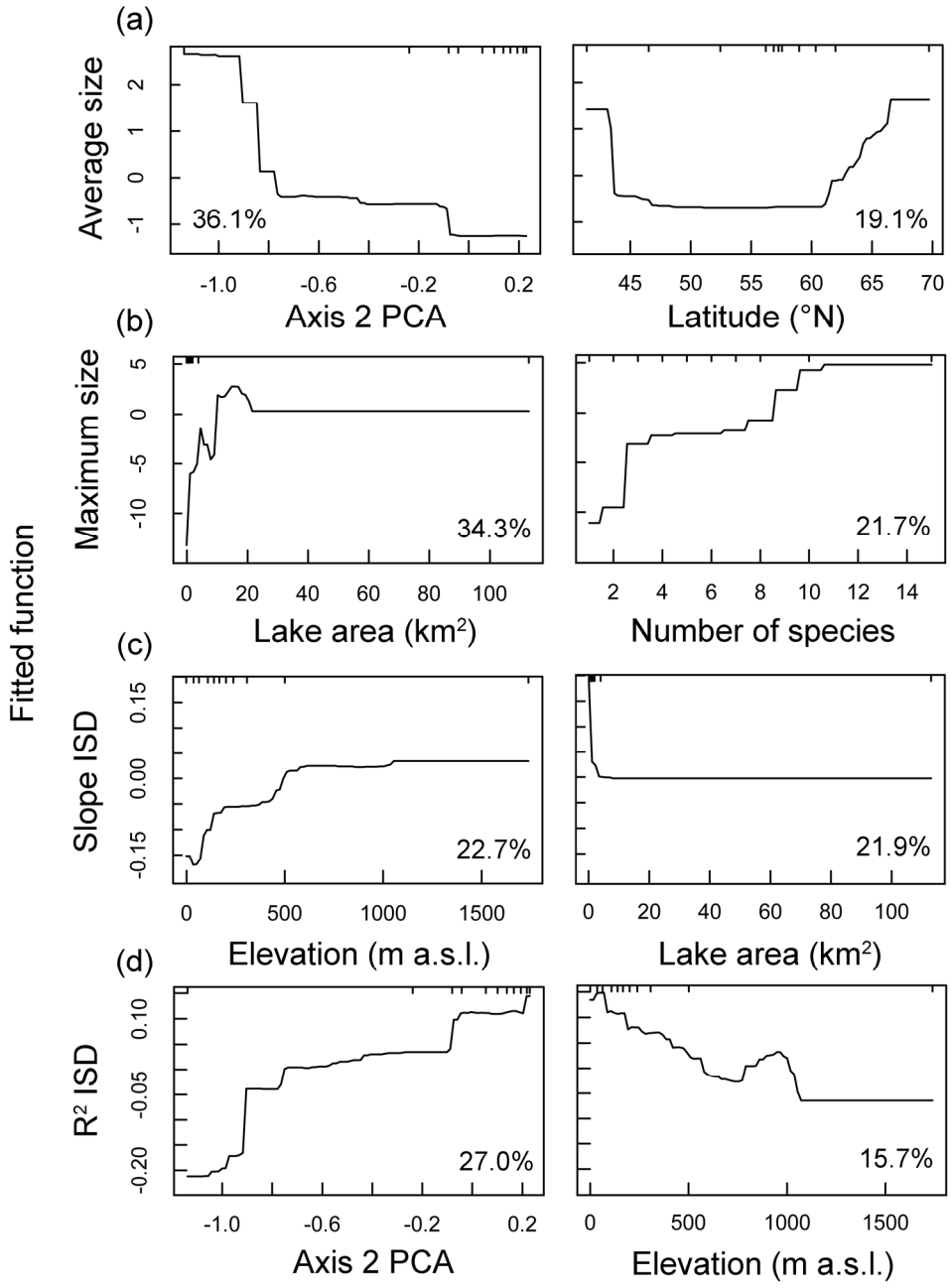

Figure 5. Partial dependence plots showing the two most influential predictor variables on the fitted function (centered around the mean) of average size (a), maximum size (b) and the slope (c) and R^2 (d) of the individual size distributions (ISD). Rug plots on the top horizontal axes indicate the distributions of the predictor variables, in deciles. Percentage values indicate the relative importance of the predictor variables in the boosted regression tree analyses.

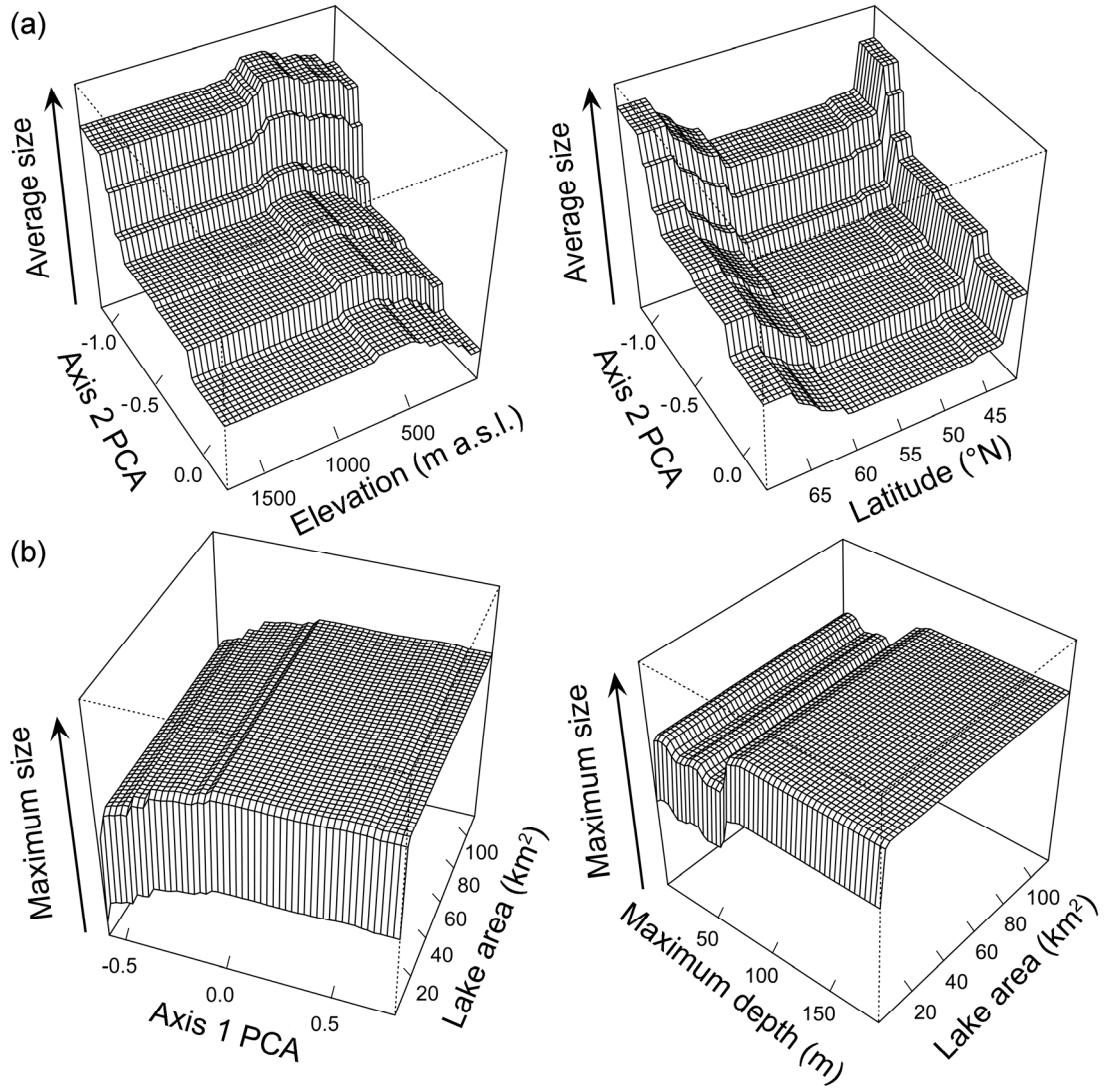

Figure 6. Three-dimensional mesh plots showing the two strongest pair-wise interactions in the boosted regression tree model for average size (a) and maximum size (b). Arrows on the z-axes indicate direction of increasing values of the size metrics.

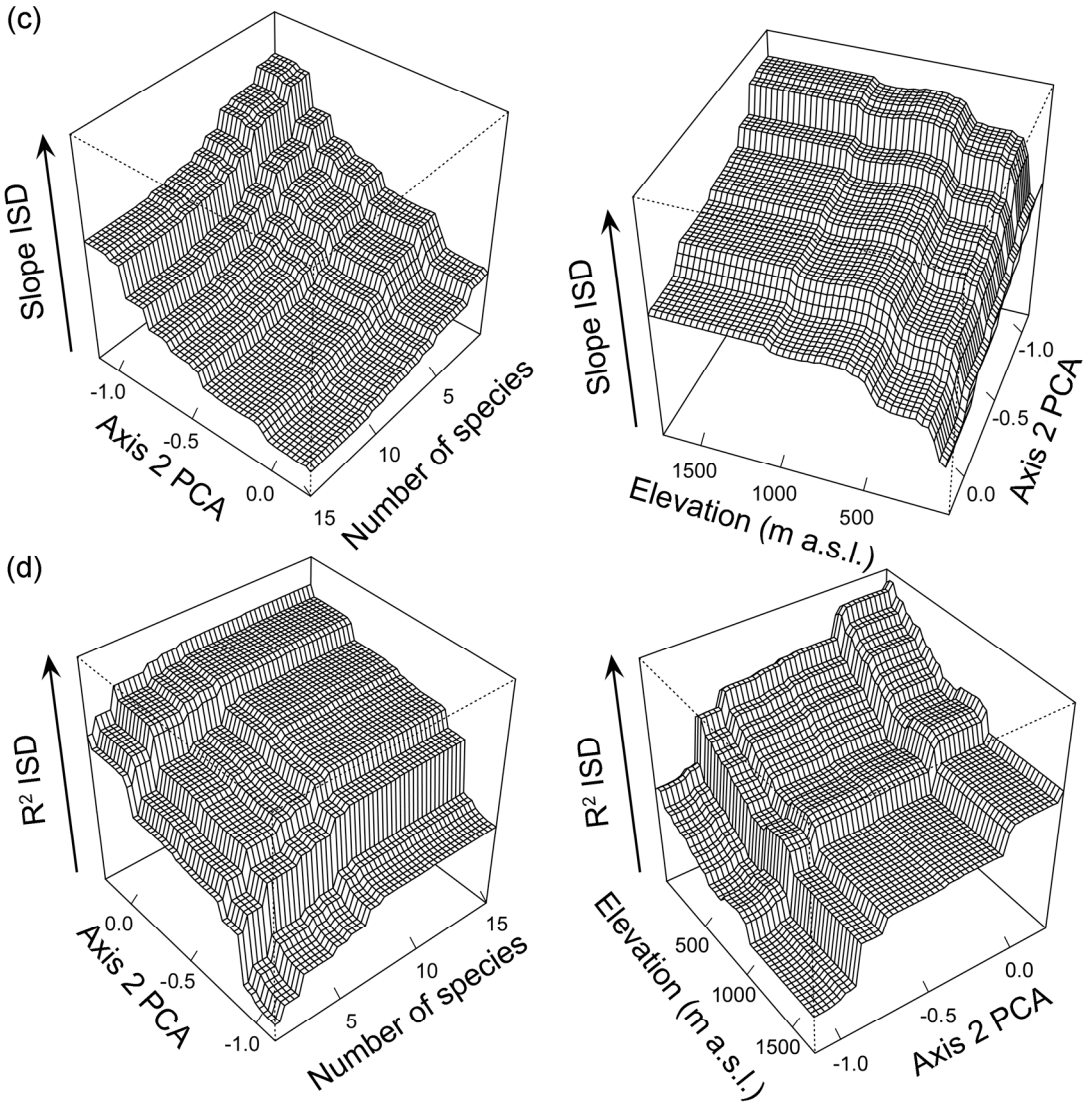

Figure 6 continued. Three-dimensional mesh plots showing the two strongest pair-wise interactions in the boosted regression tree model for the slope (c) and R^2 (d) of the individual size distributions (ISD). Arrows on the z-axes indicate direction of increasing values of the size metrics.

Table 1. Predictor variables of the 701 European lakes. Mean, minimum and maximum value and coefficient of variation (CV) are given. Site scores of the first two PCA axes are not included because their variability cannot be interpreted in the same way as for the other variables.

Predictor (unit)	Mean	Minimum	Maximum	CV
Latitude (WGS84)	56.1300	41.3953	69.6972	0.10
Elevation (m a.s.l.)	231.0	-1	1937	1.02
Area (km^2)	2.06	0.02	113	3.09
Z_{max} (m)	16.8	1	190	1.07
TP ($\mu g\ L^{-1}$)	29.3	1	561	1.78
$CLC_{natural}$ (%)	70.2	2.1	100	0.44
Species number	5	1	15	0.55

Z_{max} = maximum depth, TP = annual mean total phosphorus concentration, $CLC_{natural}$ = percentage of natural ground in the catchment area

Table 2. Relative influence of the abiotic and biotic predictor variables in the boosted regression tree models on average size (AS), maximum size (S_{max}) and slope and determination coefficient (R^2) of the individual size distributions from 701 European lakes. The rank of importance of the predictor is given in brackets.

Predictor	AS	S_{max}	Slope	R^2
Latitude	19.1 (2)	11.6 (3)	5.2 (6)	14.7 (3)
Elevation	14.8 (3)	6.6 (5)	22.7 (1)	15.7 (2)
Area	1.3 (8)	34.3 (1)	21.9 (2)	7.3 (7)
Maximum depth	13.7 (4)	4.3 (7)	11.8 (5)	9.4 (6)
Total phosphorus	0.6 (9)	4.6 (6)	1.3 (8)	2.3 (8)
$CLC_{natural}$	2.7 (7)	3.9 (8)	1.2 (9)	2.0 (9)
Species number	3.1 (6)	21.7 (2)	14.3 (4)	12.1 (4)
Axis 1 PCA	8.7 (5)	3.2 (9)	2.1 (7)	9.5 (5)
Axis 2 PCA	31.6 (1)	9.9 (4)	19.6 (3)	27.0 (1)

$CLC_{natural}$: Percentage of natural ground in the catchment area

Axis 1: Discrimination between perch- (coolwater) and roach- (warmwater) dominated fish assemblages

Axis 2: Discrimination between perch/roach- (cool/warmwater) and salmonid- (coldwater) dominated fish assemblages

The following Supporting Information is available for this article online:

Table S1. List of fish species occurring in more than five of the 701 lakes, their relative numerical abundance (%) in the total catch and their frequency of occurrence (% of 701). Pearson's correlation coefficients with the first two principal component axes are given. Correlations > 0.3 are highlighted in bold.

Scientific name	Common name	Abundance	% of 701	Axis 1	Axis 2
Abramis brama	bream	3.83	42.94	**0.360**	-0.115
Alburnus alburnus	bleak	2.37	24.96	0.210	-0.044
Ameiurus melas	black bullhead	1.64	4.42	0.118	-0.120
Anguilla anguilla	eel	<0.01	2.00	0.081	-0.048
Aspius aspius	asp	<0.01	0.86	0.071	-0.055
Barbatula barbatula	stone loach	0.01	1.00	0.053	-0.131
Barbus barbus	common barbel	0.01	1.00	0.050	-0.006
Blicca bjoerkna	white bream	4.72	21.26	**0.319**	-0.187
Carassius gibelio	prussian carp	<0.01	1.00	0.009	-0.011
Carassius carassius	crucian carp	0.05	3.85	0.055	-0.069
Cobitis taenia	spined loach	0.02	3.42	0.033	0.061
Coregonus albula	vendace	0.78	11.13	-0.050	0.047
Coregonus lavaretus	whitefish	0.43	10.84	-0.086	0.000
Cottus gobio	European bullhead	<0.01	0.86	0.024	-0.139
Cottus poecilopus	alpine bullhead	0.01	1.14	-0.039	0.005
Cyprinus carpio	carp	0.07	6.42	0.117	0.001
Esox lucius	pike	0.37	66.62	0.071	0.188
Gobio gobio	gudgeon	0.37	5.42	0.064	-0.087
Gymnocephalus cernuus	ruffe	4.59	35.66	0.191	0.038
Hypophthalmichthys molitrix	silver carp	0.01	0.86	0.052	-0.089
Lepomis gibbosus	pumpkinseed	0.11	5.42	0.064	-0.003
Leucaspius delineatus	sunbleak	0.02	0.71	0.096	-0.036
Leuciscus idus	die	<0.01	0.71	0.008	0.009
Leuciscus leuciscus	dace	0.01	0.86	0.015	0.032
Lota lota	burbot	0.08	8.27	0.017	-0.266
Oncorhynchus mykiss	rainbow trout	0.05	3.14	0.011	-0.150
Osmerus eperlanus	smelt	0.31	5.42	0.007	-0.053
Perca fluviatilis	perch	43.37	93.87	**-0.870**	**0.483**
Phoxinus phoxinus	common minnow	0.09	3.71	0.021	-0.251
Rutilus rutilus	roach	32.02	81.46	**0.798**	**0.585**
Salmo trutta	brown trout	0.65	12.27	0.086	**-0.776**
Salvelinus alpinus/umbla	charr	0.66	6.99	0.046	**-0.533**
Sander lucioperca	pikeperch	1.72	21.26	0.271	-0.087
Scardinius erythrophthalmus	rudd	1.41	28.67	0.124	-0.008
Silurus glanis	European catfish	0.01	3.14	0.135	-0.093
Squalius cephalus	chub	0.09	4.99	0.064	-0.011
Tinca tinca	tench	0.11	19.83	0.084	0.068

Table S2. Predictive performance (D^2) of the boosted regression tree models on average size (AS), maximum size (S_{max}) and slope and determination coefficient (R^2) of the individual size distribution of lakes with complete information on total phosphorus (TP) and percentage on natural ground in the catchment area ($CLC_{natural}$) (n = 274). The relative influence (%) and the rank of importance of the predictor (in brackets) are given.

Size metric	AS	S_{max}	Slope	R^2
D^2 (%)	36.7	20.6	44.5	46.9
Predictor				
Latitude	15.6 (4)	12.2 (3)	7.6 (5)	16.6 (3)
Elevation	22.5 (3)	10.4 (5)	28.7 (1)	25.8 (1)
Area	5.1 (5)	14.3 (2)	23.0 (2)	10.3 (5)
Max. depth	22.9 (2)	7.4 (7)	15.1 (3)	13.7 (4)
TP	0.9 (9)	6.6 (8)	1.2 (8)	1.0 (8)
$CLC_{natural}$	1.5 (8)	8.3 (6)	1.6 (7)	0.9 (9)
Species number	4.0 (6)	23.4 (1)	7.7 (6)	6.1 (6)
Axis 1 PCA	2.8 (7)	5.7 (9)	1.1 (9)	1.4 (7)
Axis 2 PCA	24.7 (1)	11.9 (2)	14.0 (4)	24.4 (2)

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